BOTANY
PRINCIPLES AND PROBLEMS

BY

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(*Frontispiece*)
All four main divisions of the plant kingdom are represented in this picture.

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To My Mother

PREFACE

The present volume, an outgrowth of experience in presenting to college freshmen a course in elementary botany, endeavors to set forth somewhat briefly and concisely the more important facts concerning the morphology, physiology and classification of plants, and to provide a body of problem material which may be of assistance in stimulating thought and in promoting class discussion.

The consideration of structure and function in the earlier portions of the book is confined mainly to the seed plants, and the distinctive characteristics of the other members of the plant kingdom are discussed in the last five chapters. Should the course be too brief to take up these groups in detail, Chapter XIII, which deals with the main events in the history of the plant kingdom and the important features of its various divisions, may perhaps be used to give the student an idea of the kingdom as a whole. In view of the importance of the soil in the life of plants, and in order to emphasize the fact that living things cannot be understood without a knowledge of their environment, an early chapter is devoted entirely to the soil itself. The increased interest in matters pertaining to inheritance has warranted a special chapter on heredity and variation; and a chapter is also devoted to organic evolution, emphasizing its botanical aspects. The chapters have been so written as to be separately understandable and may readily be taken up in some other order than that in which they are here presented. The text is not primarily designed for agricultural students but many of the questions naturally involve a practical application of botanical principles and will perhaps commend themselves especially to those whose interest in botany is chiefly agricultural.

The rather extensive lists of "Questions for Thought and Discussion", which are perhaps the most novel feature of the present volume, have resulted from an attempt to stimulate within the student an attitude of interest, of curiosity and of critical thought toward the multitude of problems which plants present, and thus to provide him with a clearer insight into the way in which plants are constructed and function, and a firmer

command of botanical science in general, than can be given him merely through a series of lectures and recitations. Anyone who has mastered the facts presented in the text and who has at his command a reasonably broad body of experience, ought to be able, through the exercise of a little thought, to prepare satisfactory answers for all of them. "Thought questions" are by no means new in botanical pedagogy, but it is believed that no previous text has employed them to quite such an extent as does the present one. It is hoped that their inclusion here may encourage a method of class-room procedure more satisfactory than the common but somewhat outworn practice wherein a monopoly of thinking and talking is enjoyed by the instructor, and the student is chiefly required to memorize a series of what often seem to him to be unrelated facts. The "Reference Problems" are designed to send the student occasionally to other sources of information than his textbook, and thus to broaden his point of view and dispel from his mind the comfortable assurance that any particular authority may be infallible.

To all those who have been of assistance in the preparation of the book the author desires to express his sincere thanks. Many of his colleagues have contributed helpful suggestions and information in matters relating to their special fields, and to Professor G. S. Torrey is he especially indebted for advice and assistance during the course of the work. Professor Torrey and Dr. L. C. Dunn have been good enough to read and criticize portions of the manuscript. A. I. Weinstein has been helpful in many ways. Professor M. L. Fernald of the Gray Herbarium kindly supplied the data used in Figs. 131, 132 and 133. To Professor B. M. Davis of the University of Michigan and Professor J. W. Harshberger of the University of Pennsylvania the author is under obligation for their courtesy in providing material and facilities for the preparation of a number of the figures. He is also much indebted to his wife for frequent assistance during the preparation of text and illustrations.

The great majority of the illustrations are original. They are the work of several individuals, to whom the author is grateful for hearty coöperation. Mrs. Grace Griffin Hosking is responsible for Figs. 21, 22, 26, 66, 81, 99, 135, 136, 141, 142, 144, 145, 146, 147, 149, 151, 152, 153, 157, 158, 159, 160, 161, 174, 181, 184, 185, 187, 188, 189, 196, and 216; H. C. Creutzburg for Figs. 20, 45, 47, 96, 162, 166, 167, 169, 170, 175, 177, 178, 180, 182,

186, 190, 191, 193, 209, 211, and 213; Mori Uyehara for Figs. 154 and 155; E. J. Slanetz for Fig. 18, and A. I. Weinstein for Figs. 137 and 143, as well as for Figs. 111 and 230 from his unpublished work. The other original drawings, some ninety in all, are by the author. He is indebted to Professor W. F. Ganong and the Macmillan Co. for the use of four figures from "A Textbook of Botany for Colleges"; to Professor W. F. Ganong and Henry Holt and Co. for the use of two figures from "The Living Plant", and to Dr. C. S. Gager and P. Blakiston's Sons and Co. for the use of four figures from "The Fundamentals of Botany". To the United States Forest Service, the United States Forest Products Laboratory, the Desert Laboratory of the Carnegie Institution, the Brooklyn Botanic Garden, the editors of the *Journal of Heredity* and of *Genetics*, Dr. A. J. Grout, Professors E. B. Babcock and R. E. Clausen, Dr. M. A. Howe, Professor I. W. Bailey, Professor E. W. Berry, Professor M. L. Fernald, and Professor G. S. Torrey the author is indebted for original illustrations or permission to use published ones. A few familiar figures have also been taken from some of the older texts.

The author will be very glad to welcome criticisms and suggestions, particularly those which relate to the employment of the Questions and Problems in the conduct of class work.

E. W. Sinnott.

Connecticut Agricultural College,
July, 1923.

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TO THE STUDENT

Botany has sometimes been spoken of rather slightingly as the "feminine" science, and indeed in the minds of many people it is chiefly associated with pleasant exercises in learning the names of wild flowers, or with quaint individuals who wander absentmindedly in the woods and fields, trowel and tin box in hand, and who rejoice in the use of long and unpronounceable Latin words. That such a conception of the science of botany is wholly inadequate, a study of the following pages should amply prove. Plants are far more than interesting playthings. They are a conspicuous and inescapable part of the world we inhabit. They make life possible for us by providing food, clothing, fuel, shelter, and many other necessities. More important still, they are *alive* and thus endowed with those remarkable qualities which have always made all living things eagerly studied by man, not only for their own sake but for the light which they throw on many human problems. If education is indeed an understanding of our surroundings, surely no one should pretend to be educated well who is unfamiliar with plants and their activities.

A college textbook or a college course in any branch of biology, however, ought to do something more than give familiarity with a mass of facts, no matter how important they may be. It should develop in us the *right attitude toward these facts*. This attitude—the truly *scientific* attitude—is both critical and inquisitive. It should enable us to find our way to the truth through a maze of facts. This is the attitude which distinguishes a truly educated man from one who is merely knowledge-crammed, and a lack of it is responsible for much of the loose thinking and false reasoning with regard to biological problems which is indulged in by many people.

Let us see what this attitude demands and how it may best be attained. We are all obliged to acquire a mass of information if we are to live successfully. We must know the character of the various things which we eat and wear, the operation of countless devices which we use, the rules and habits of other people, the

manifold concerns of our particular occupations, together with countless other facts and details. The world is continually asking us "*what?*", "*where?*", "*when?*" and "*how?*"; and we are continually answering it as best we may. For most people the ability to reply successfully to these questions is sufficient, and they desire nothing further. In a course in elementary botany, such would be content merely to learn the facts about plants so that they might pass the inevitable examination. There are always a few, however, who are not satisfied thus to take everything for granted, as a lesson to be learned. They want to ask the world a question in their turn, and their question is far more profound. It is "*why?*" They crave not merely knowledge but *understanding*. They want to penetrate the array of facts to the laws upon which these facts rest. To this honorable band have belonged all great thinkers and philosophers, all discoverers and explorers, all who have helped to bring mankind upward from thoughtless savagery to rational civilization. These men have often been ridiculed, frowned upon or even persecuted for their presumptuous curiosity, but they have persisted through the ages in that insatiable inquisitiveness which has led them to challenge the world, not to accept it; to penetrate its secrets rather than take all for granted. Their spirit animates every true scientist and every really educated man today.

But the scientific attitude is not mere inquisitiveness. Brutes often have plenty of that. Many people are idly curious and will accept any explanation offered them. The scientist must go beyond this. Among the many answers which come back to him when he asks "why?" he must be able to discriminate, to separate the true from the false. He must weigh accurately and without prejudice the claims of the various theories which have been put forward to answer his questions. He must remain skeptical and unconvinced until adequate proof is at hand. He must satisfy his reason. In the best sense of the word, he must be *critical*.

This attitude of critical curiosity is hard to gain and still harder to maintain actively. It is a useful practice, particularly when encountering a subject which is new or unfamiliar, to prod ourselves continually with questions and problems which it brings up, not merely accepting someone else's assertion but trying things out for ourselves. The college student, above all men, should thus learn to be his own Socrates. It is for this

purpose that the list of "Questions for Thought and Discussion," which will be found at the end of each chapter of the following text, has been gathered. The student can try his hand at these, and if he has first mastered the comparatively few facts presented in the text he should have no great difficulty. The answers to some are easy, almost obvious. Others may be harder to find but will be worth more in the finding. By frequent practice in this sort of exercise he will not only develop and keep sharp his curiosity and his ability to reason and discriminate—the most important ends for him to gain in such a course as this—but he will acquire almost unconsciously a far more thorough understanding of the structures and functions of plants than he could by merely attempting to memorize a list of facts. The tonic of curiosity and the fresh air of skepticism are sovereign aids for maintaining our minds in that state of health and vigor in which they can steadily assimilate a rich diet of knowledge without becoming sluggish and over-fed.

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BOTANY: PRINCIPLES AND PROBLEMS

CHAPTER I

THE SCIENCE OF BOTANY

Botany may be defined as that field of precise and classified knowledge—that *science*, in other words—which deals with plants.

Together with the members of the animal kingdom, plants are distinguished from all other objects by the fact that they are *alive*. Botany and Zoölogy, the sciences which treat of these two great groups of living things, are therefore closely related to one another, dealing with many facts and facing many problems in common; and together they constitute the broader scientific field of Biology, which is concerned with the study of Life in its various manifestations. Of all branches of human knowledge, this science of life is perhaps the least understood and the most important. Between lifeless things and living things exists a great gap which, despite our advances in knowledge, we are as yet unable to bridge. Intricate machines and complex chemical substances are familiar products of manufacture, but never have we succeeded in constructing anything alive out of non-living material. Plants and animals thrive, multiply and die before our eyes, but as to many of the processes which lie behind these outward activities we are still in almost complete ignorance. We may describe, but often cannot explain. Moreover, living things are not fixed and constant in their characteristics but have undergone profound changes, from simpler beginnings in ages long past to the enormous variety and complexity which they exhibit today; but what has been their origin, or how and why they have progressed to their present condition, are questions for the future to answer. It is this baffling and unexplained quality in life which always has keenly stimulated the curiosity of man; and

since he himself is a living being, much of his speculation and philosophy has naturally centered around problems which, in a broad sense, are biological in their nature. The task of the biologist in extending the field of our scientific knowledge of *plants and animals therefore assumes added significance from its* relation to some of the most profound questions with which mankind is confronted. As an integral part of the science of biology, botany has already made notable contributions to our knowledge of living things; and so long as man preserves that insatiable *curiosity toward Nature which has distinguished him as a thinking* being, he will always in some measure be a student of plants.

Aside from its theoretical interest, botany is also of very great practical importance to mankind because plants touch human activities so intimately and in so many ways. All food which nourishes animals and man, and makes life possible, comes originally from a union of water and a simple gas, carbon dioxide, in the leaves of green plants. Our clothing, our fuel, our drugs and countless other necessities of civilized life are likewise contributed, directly or indirectly, by members of the plant kingdom. As a means of quickening that intelligent appreciation of his surroundings which should distinguish every educated man, a scientific knowledge of plants is therefore of the utmost value.

The Subdivisions of Botany.—Owing to the great mass of diverse facts which it has accumulated and the many points of view from which its problems have been attacked, every major science has necessarily become divided into sub-sciences, each of which makes its particular contribution to the whole. Thus *botany is composed of a series of specialized sciences.* Three of these—Systematic Botany, Plant Morphology and Plant Physiology—are most worthy of note and are themselves subdivided and recombined still further.

Systematic Botany or *Plant Taxonomy* is concerned with the *names of plants and the classification of the vegetable kingdom.* Its object is to identify by name and description all the kinds of plants which can be distinguished, and to arrange them, according to their natural relationships, into those groups which we call species, genera, families and orders. Since these relationships can be determined only *after a knowledge of evolutionary* history, the science of *Plant Phylogeny*, which endeavors to trace the genealogy of the plant kingdom, is an important adjunct to systematic botany.

Plant Morphology is concerned with the form and structure of plants. Its object is to describe the construction and organization of the plant body and to trace underlying similarities in form between various plant groups. Under morphology are included *Anatomy*, dealing with internal structure in general; *Histology*, with the more minute internal structures; *Cytology*, with the structure of the cell; *Embryology*, with the development of the individual, and *Experimental Morphology*, with the causes which determine form and structure.

Plant Physiology is concerned with the functions of plants. Its objects are to describe and explain the various activities by which the life of the plant is maintained and transmitted to its offspring. Physiology obviously underlies the other subdivisions of botany since it touches the very process of living. A branch of physiology particularly active today is *Genetics*, which deals with the problems of inheritance.

Aside from these three major sub-sciences there are other fields of botany which deserve mention. *Plant Ecology* is concerned with the relations between plants and the various factors of their environment such as soil, climatic conditions and living organisms; and, in particular, with the modifications of structure and function which enable them to react successfully to changes in their surroundings. Ecology necessarily involves both morphology and physiology, as well as certain of the physical sciences. *Plant Geography* is concerned with the geographical distribution of plants, and is intimately related both to systematic botany and to ecology, as well as to geology and geography. *Palaeobotany* is concerned with the structure and relationships of fossil plants, and thus touches systematic botany, morphology, and geology.

In addition to all these aspects of botany, most of which are theoretical rather than practical in their bearing, we should not fail to mention the great group of sciences concerned with the utilization and culture of plants. *Economic Botany*, in its narrower sense, is a study of those plants which are valuable to man and of the uses to which they are put. The various sciences commonly grouped under Agriculture (*Soil Science*, *Agronomy*, *Horticulture*, *Plant Pathology*, and many others) together with *Forestry*, *Pharmacology* and their subsidiaries, are eminently practical, and their close relationship to botany is sometimes overlooked. They are nevertheless integral parts of our science,

and for their successful pursuit demand a sound knowledge of botanical principles. Everyone who is concerned with plants from a scientific point of view, whatever his purpose or profession, is rightfully to be called a botanist.

The History of Botany. *The Classical Period.*—Botany as we know it today is the result of a long term of observation

Fig. 1.—Aristotle, 384–322 B.C.

and inquiry. As do so many other sciences, it looks back to the fertile speculations of the Greeks for the first definite expression of its problems and principles. The "nature" of plants was studied by Aristotle (384–322 B.C., Fig. 1) who saw clearly certain of the broader problems of plant and animal life, and whose sagacious comments thereon are still worthy of our attention. It is his disciple Theophrastus of Eresus (371–287 B.C.), however, whom botanists have generally regarded as *the father of their science.* This keen naturalist accumulated a great mass of information with regard to plants and discussed their various characteristics. Rome also had her share in the development of plant science, notably through the contributions of Pliny the Elder (23–79 A.D.), whose "Natural History,"

a compendium of facts and fancies about living things, was long a storehouse of botanical information. Dioscorides, living at about the time of Nero, studied plants for their medicinal properties and holds an important place historically in both botany and medicine.

The Herbalists.—After this, its classical period, botany went into that profound eclipse suffered by all sciences during the Middle Ages. The teachings of the ancient masters were jealously preserved and were commented upon and dissected, but the thought of extending knowledge by direct observation and experiment was held to be almost sacrilegious. About the beginning of the sixteenth century, however, a group of open-minded men living in the Rhine valley and its adjacent regions undertook to explore the plant kingdom afresh for themselves. They were interested in plants chiefly for the curative virtues to be found therein, and, paying scant attention to the doctrines and dogmas of the ancients, they went about describing and drawing with fidelity the various kinds of plants which flourished in their native countries. From the numerous herb-books or "Herbals" in which the resulting discoveries were published, these pioneers have been known as the "Herbalists". They endeavored to distinguish clearly the different species from one another, and proposed certain crude methods of classifying the plant kingdom. So unprejudiced and free from the conventional dogmatism of the age was their whole attitude that the Herbalists are generally regarded as the fathers of modern botany.

The Modern Period.—The first extensive and thorough classification of plants was that proposed in 1583 by the Italian botanist Cesalpino (1519–1603). Combining an acquaintance with the ancients and an intimate first-hand knowledge of plants, he laid down certain principles which were the basis of systematic botany for many years. Modern taxonomy, however, dates from the publication of the "Species Plantarum" by the great Swedish naturalist Linnaeus (1707–1778, Fig. 2), in 1753. In this monumental book all the plant species known at that time were named, carefully described, and arranged according to a definite system.

Although the early work in botany was thus concerned chiefly with taxonomy, the study of plant structures was not neglected. Grew (1628–1711) in England, and Malpighi (1628–1694) in Italy, were keenly interested in the internal construction of the

plant body, and their works on "phytotomy" laid the foundation for our modern knowledge of plant morphology. The continued improvement in the compound microscope made possible more complete and accurate knowledge of the way plants are constructed, and led to the formulation by Schleiden, in 1838, of the Cell Theory, which states that the cell is the unit of structure in plants and that protoplasm is its essential constituent. From this beginning, modern anatomy and cytology have added a great

FIG. 2.—Carolus Linnaeus (Carl von Linné), 1707–1778.

body of facts to our knowledge of the structure, growth, and reproduction of the plant body.

The ancients and the early modern botanists for the most part had fanciful and inaccurate ideas as to the way in which the plant carried on its various functions, an ignorance largely due to the undeveloped state of the sciences of physics and chemistry at the time. It was not until the latter part of the eighteenth century that modern plant physiology became definitely established. Oxygen was discovered by Priestley in 1774, and five years later a Dutch physician, Ingenhousz, observed that green plants in the light take in carbon dioxide and give off oxygen, and that all plants give off a certain amount of carbon dioxide. These gas exchanges were accurately measured by de Saussure in the early years of the nineteenth century, and some of the

important facts of plant physiology thus became established. Since that time the development of modern chemistry and physics has made possible a steady advance in our knowledge of the physiological processes of living things.

The publication of the "Origin of Species" by Charles Darwin (Fig. 3) in 1859 resulted in a general acceptance among scientists of the theory of evolution. A recognition of the fact that the

FIG. 3.—Charles Darwin, 1809–1882.

plants of today have been slowly developed from simpler ancestors has had a profound effect upon botanical science and has stimulated a great interest in reconstructing the "family tree" of the plant kingdom and establishing a really "natural" system of classification, based on actual relationship, to replace the artificial systems of Linnaeus and his predecessors. It has led also to a more intensive study of the laws of variation and inheritance, and the causes and method of evolution. This has been encouraged still further by the discovery of Mendel's Law of Inheritance, propounded in 1866, disregarded for many years, and finally brought to the attention of biologists again in 1900.

The present state of the science of botany, then, is the result of a long period of slow development, in which truth has been gradually separated from error and our present vast store of facts amassed. With each advance, new questions have arisen and new fields of investigation have opened, until the science has

broadened from a mere discussion of the names and properties of medicinal herbs to an attack upon the fundamental problems of life itself

QUESTIONS FOR THOUGHT AND DISCUSSION

1. Name three important differences between a typical plant and a typical animal.

2. Which do you think is the most important of all the various contributions made by plants to man's welfare?

3. What great industries are founded primarily on plants?

4. Could man get along better without his domestic animals or without his cultivated plants? Explain.

5. What is the difference between a botanist and a person who is merely interested in plants?

6. Would you consider the following to be botanists:

A farmer?	A cabinet maker?
A florist?	A forester?
A sanitary engineer?	A landscape architect?

7. If a person makes a careful study of all the species and varieties of wheat, classifying them and finding their correct names, in what field of botany is he at work?

8. If he studies the structure of the wheat stem, in what field of botany is he at work?

9. If he studies the manner in which food is manufactured by the wheat plant, in what field of botany is he at work?

10. If he studies the ways in which wheat plants respond to changes in their environment, in what field of botany is he at work?

11. If he studies inheritance in wheat, in what field of botany is he at work?

12. If he studies the geographical distribution of wheat, in what field of botany is he at work?

13. If he studies the various uses to which wheat may be put, in what field of botany is he at work?

14. In what ways may a knowledge of botany be of value in everyday life?

15. Name a definite and specific problem, of practical, "dollars-and-cents" importance, in agriculture or any other line of industry, for

the solving of which a knowledge of systematic botany would be valuable.

16. Name such a problem in which a knowledge of plant morphology would be valuable.

17. Name such a problem in which a knowledge of plant physiology would be valuable.

18. Name such a problem in which a knowledge of plant genetics would be valuable.

19. Name such a problem in which a knowledge of plant ecology would be valuable.

20. Give an instance of a practical situation in which a man with a knowledge of both the scientific and the practical sides of agriculture would have an advantage over a man who knew only the practical side. Why would he have this advantage?

21. How is a knowledge of chemistry important to a botanist?

22. How is a knowledge of physics important to a botanist?

23. How is a knowledge of meteorology important to a botanist?

24. How is a knowledge of geology important to a botanist?

25. Why was systematic botany the first aspect of botany to be studied scientifically?

26. Plants have always been used far more for food than for medicine, but despite this fact, the science of botany in its early days was almost entirely in the hands of men interested in medicine rather than in agriculture or any other branch of practical science. How do you explain this?

27. Why was a knowledge of the minute structure of plants impossible for the ancients to acquire?

REFERENCE PROBLEMS

1. What is meant by a *science?*

2. State briefly the doctrine of Spontaneous Generation and explain why it is no longer accepted by scientific men.

3. The following "applied" sciences are all closely related to botany and are founded upon it. With what does each deal?

Horticulture	Forestry
Agronomy	Pharmacology

4. Summarize the life and work of Aristotle and state his important contributions to botany.

5. Summarize the life and work of Linnaeus and state his important contributions to botany.

6. Summarize the life and work of Darwin and state his important contributions to botany.

7. What change in geological theory occurred at about the same time that the theory of evolution won wide acceptance (in the latter half of the nineteenth century)?

8. Give the derivation of each of the following terms and explain in what way it is an appropriate one:

Taxonomy	Physiology	Ecology
Morphology	Phylogeny	Genetics

CHAPTER II

INTRODUCTORY SURVEY

Before commencing an intensive study of any aspect of botanical science or of any particular problem which deals with plants, it will be well for us to make a brief survey of the plant kingdom as a whole, and of some of the more important structures and functions of plants in general.

The Plant Kingdom.—About 250,000 different kinds or *species* of plants have been discovered and described, and every year botanical exploration and careful study bring more of them to our knowledge. We have seen that the problem of systematic botany is to name this host of plants and to arrange and classify its members in a logical system. Over many of the details of such a classification difference of opinion still exists, but there is now rather general agreement as to the main groups into which the plant kingdom should be divided. Four such divisions are commonly recognized:

A. *The Thallophytes.*—These are lowly plants, various in their structure, activities, and methods of reproduction, but agreeing in the possession of a simple body without roots or leaves and in multiplying by single-celled *spores.* The majority of Thallophytes inhabit water or moist places and are small and soft-bodied plants.

There are two main series of Thallophytes: The *Algae* (Fig. 4), which possess the green pigment *chlorophyll* and are thereby able to manufacture their own food, and which include all the seaweeds and their fresh-water allies; and the *Fungi* (Fig. 5), which lack chlorophyll and consequently are obliged to obtain their food from living animals and plants or from dead organic material. Here belongs the vast array of bacteria, molds, blights, rusts, toadstools, mushrooms, and similar plants, many of which live as parasites and are often the cause of serious diseases of man and the lower organisms.

B. *The Bryophytes* or Moss Plants.—These plants are distinguished from the Thallophytes chiefly by their more highly

developed sexual structures and their more complicated methods of reproduction. The plant body of the Bryophytes has no roots, and in many cases consists of only a flat, strap-like mass of green tissue, but the higher members of the group possess very simple stems and leaves. The plants are small and inconspicuous, and generally thrive best in moist situations. Bryophytes are subdivided into the simple and lowly *Liverworts* (Hepaticae) and the commoner and more highly specialized *Mosses* (Musci, Fig. 6).

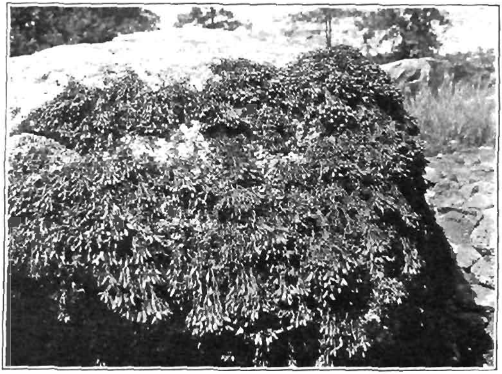


FIG. 4.—An Alga. One of the rock-weeds (*Fucus spiralis*) growing on a rock between tide-marks. (*Photo by M. A. Howe*).

C. *The Pteridophytes* or Fern Plants.—These possess true roots, stems, and leaves, essentially similar in structure to those of the Seed Plants, but they still reproduce by spores rather than by seeds. Compared with Bryophytes, the plant body is large and vigorous, and it is well adapted to life on land. The three important subdivisions of the Pteridophytes are: The *Ferns* (Filicales, Fig. 7), possessing large and feathery leaves on the backs of which the spores are produced; the *Club Mosses* or *Ground Pines* (Lycopodiales), which have spore-bearing cones, solid stems and scale-like, spirally arranged leaves; and the *Horsetails* (Equisetales) also possessing cones but with jointed, hollow stems and minute, whorled leaves.

D. *The Spermatophytes* or Seed Plants.—The dominant and familiar portion of the earth's vegetation today consists of these plants, which are well adapted for life on land and often attain

Fig. 5.—A Fungus. One of the gill fungi, *Pleurotus*, growing on a log.

great size. Their distinctive feature is the production of a complex, many-celled reproductive body, the *seed*, in which is contained an embryo plant and a supply of stored food.

Seed Plants are very numerous and exceedingly varied in form and structure, ranging from small and delicate herbs to huge trees over three hundred feet tall. They are the most conspicuous and best known of all the divisions of the plant kingdom, and provide the great bulk of the foods, timbers, fibers, and other vegetable products which form the basis of our civilization.

FIG. 6.—A Moss. A hair-cap moss, *Polytrichum juniperinum*, with ripe capsules. (*From A. J. Grout, "Mosses with Lens and Camera." Copyright by the author*).

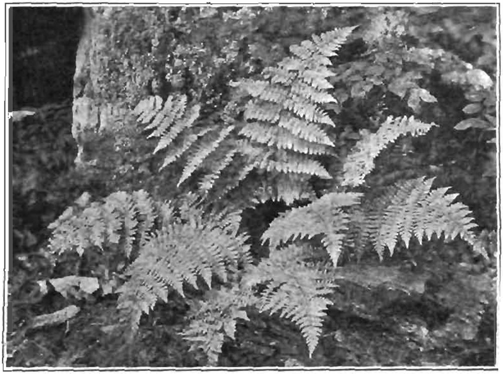


FIG. 7.—A Fern. One of the shield-ferns (*Aspidium spinulosum*).

Two major subdivisions of the Seed Plants are recognized: The *Gymnosperms* (Fig. 8), which have primitive, often cone-like flowers and bear their seeds openly exposed on scales as

Fig. 8.—A Seed Plant (Gymnosperm). Fir tree (*Abies nobilis*).

in our common coniferous trees; and the *Angiosperms* (Fig. 9), in which there is usually a typical flower with its various floral parts, including an *ovary* in which the seeds are enclosed during their development. There are only about 450 species of Gymnosperms living today, but the Angiosperms are an enormous

group of more than 130,000 species and are our most familiar plants. They are divided again into two main groups, the

FIG. 9.—A Seed Plant (Angiosperm). Hawthorn tree (*Crataegus*).

Dicotyledons and the *Monocotyledons*, which differ from each other in the structure of the seed, leaf, stem, and flower.

Underlying the differences by which these various groups are distinguished from one another, there are many fundamental similarities in structure and function which are common to all plants; but the marked changes which appear as we pass from the lowest to the highest types make very difficult a concise description of the characteristics of the plant kingdom as a whole. It will therefore, be profitable for us to confine our attention, at first, mainly to those plants which are most familiar to everyone and of most obvious and immediate interest to man—the Seed Plants. The sciences of morphology and physiology, as exemplified by the Seed Plants, will accordingly be the chief object of study in the first portion of this book. In these early chapters we should be careful to remember that only one division of the plant world—albeit the most important one—is being considered, although many of the facts and principles there established are, of course, valid for all plants. In the last chapters of the text we shall discuss in some detail the lower members of the vegetable kingdom, and the respects in which they differ from each other and from the Seed Plants.

The great variety of plant types and the diversity of conditions under which they live renders it difficult to make general statements about plants which are universally true, for exceptions to any such statement may usually be found. Indeed, variability is one of the most notable characteristics of all life. The student should therefore bear in mind that many of the facts and principles set forth briefly and simply in an elementary text are to be taken as true for typical cases and under ordinary conditions, and he should be careful not to accept them as necessarily and universally true for all plants and under all conditions. Living things are too complicated to be described completely in simple formulas.

The Structures and Functions of Plants.—A notable characteristic of plants, which they share with all other living things, is their very definite bodily form. This form is not merely external or accidental but is the mark of a fundamental organization or "division of labor" within the plant itself. The individual is made up of a series of distinct and visibly different parts, each of which possesses a specific shape and performs a specific function (Fig. 10). These parts are called *organs*. The root, the stem, the leaf, the flower, the fruit, and the seed, as well as

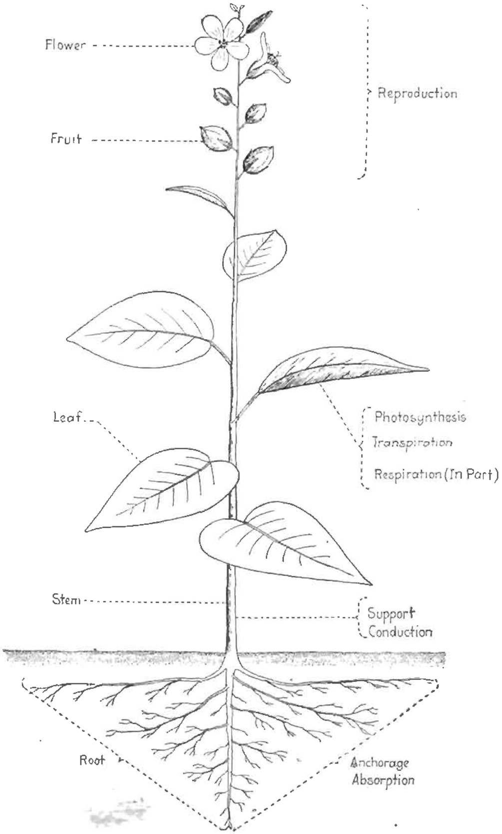


FIG. 10.—The important structures and functions of a seed plant, illustrated diagrammatically.

the various subordinate parts of which each may be composed, such as bud, petiole or stamen, are some of these organs.

The organ, in turn, is not homogeneous in texture and construction but is made up of a group of *tissues*, each of which performs a particular task contributory to the general function of the entire organ. Thus a stem may be composed of bark tissue, cortical tissue, bast tissue, cambial tissue, woody tissue, and pith tissue, each of them playing some role in the economy of the stem as a whole. One type of tissue may, of course, enter into the construction of several organs; for there is woody tissue, for example, in the root, the stem, and the leaf.

A tissue, in turn, is an aggregation of *cells*, those ultimate units of structure and function in all organisms. Each plant cell is a minute but distinct bit of living substance, or *protoplasm*, with nucleus, plastids, sap-cavity, and other structures of its own, and is usually enclosed in a cellulose wall. The individual plant may, indeed, be regarded as a huge colony of minor individuals, the cells, each performing some particular function in the whole and all bound together to their mutual advantage. A knowledge of the structure and activities of cells is the foundation upon which our understanding of plants and animals must be built.

The Root and Its Functions.—The *root* is that organ which anchors the plant in the soil and which absorbs therefrom water and simple inorganic nutrient materials. Aside from these primary functions, it frequently serves as a storehouse for reserve food and often assumes other secondary duties. The root system may consist of a single strong *tap-root*, with weak lateral branches, or of a much-branched series of smaller *fibrous roots*. The function of absorption takes place in minute *root-hairs*, delicate outgrowths from the surface cells just behind the young and growing root-tip. Into these root-hairs, by the process of *osmosis*, pass water and dissolved substances (chiefly nutrient mineral salts) from the soil.

The Leaf and Its Functions.—The typical leaf is a broad and thin structure, green in color and freely exposed to air and light. Its essential portion, the *blade*, is usually supported by a stalk, the *petiole*. From the leaf tissues, the water which has entered the root and ascended the stem is evaporated in the process of *transpiration*. Most of the internal cells of the leaf possess a green pigment, *chlorophyll*, which can utilize the energy of light

to combine carbon dioxide (coming from the air) and water (coming from the soil) into *grape sugar,* a simple carbohydrate food. This process of *photosynthesis* is entirely confined to green plants. By it is manufactured all the food which sustains the lives of plants and animals and of man himself, for all the complex foods with which we are familiar have been built up by progressive modifications of grape sugar produced in green leaves.

The Stem and Its Functions.—The stem normally holds aloft in the air the leaves and reproductive organs, and serves as a highway for transportation of water and nutrient materials from the root to the leaf, and of manufactured food from the leaf to other parts of the plant body. Stems may be comparatively small and soft, as in herbaceous plants, or stout and woody, as in trees and shrubs. They are occasionally modified for special functions, such as food-storage or photosynthesis.

The Reproductive Organs and Their Function.—The sole function of these organs is the production of offspring, through which the life of the plant may be transmitted to succeeding generations. The *flower,* typically composed of *sepals, petals, stamens,* and *pistil,* is concerned with effecting *fertilization,* or the union of male and female sexual cells; the *fruit* protects the growing seeds and often aids in their dispersal, and the *seeds* are young plants themselves in embryo, protected by a coat, provided with a supply of food, and ready to begin their independent growth and development whenever favorable conditions appear.

Metabolic Processes.—Certain physiological activities of the plant are not confined to any one organ but are characteristic of living substance or protoplasm wherever it may be. Notable among these are *digestion,* whereby food is rendered soluble; *assimilation,* whereby such digested food is incorporated into protoplasm, and *respiration,* whereby the supply of energy necessary for the plant's activities is released through the breaking down of living tissue, with the consequent absorption of oxygen and liberation of carbon dioxide.

QUESTIONS FOR THOUGHT AND DISCUSSION

28. There are almost as many species of Thallophytes as of Seed Plants, but the latter are much more familiar to most people than are the former. Why?

29. Which of the four main divisions of the plant kingdom do you believe is the oldest? Why?

30. Which of these four divisions contains the most plants useful for food?

31. In which of these four divisions are the largest plants found? In which the smallest?

32. To which of these four divisions do plants growing in the ocean chiefly belong? To which do land plants chiefly belong?

33. Name some Thallophytes which are useful to man and some which are harmful. Name some Spermatophytes which are useful and some which are harmful.

34. Which of the four divisions contains the largest number of plant species which are harmful to man and to his domestic animals and plants? Which contains the largest number of useful species?

35. Bryophytes and Pteridophytes have much fewer species than either Thallophytes or Spermatophytes. What reason can you suggest for this fact?

36. Under what climatic conditions are Pteridophytes most conspicuous and abundant?

37. What are the advantages of organization (the "division of labor") in a plant?

38. Which of the four main divisions of plants do you think shows the highest degree of organization within its plant body?

39. In general, do you think that it has been the most highly organized or the less highly organized plants which have been most successful? Explain your answer.

40. Why are living things called "organisms"?

41. Are the most important agricultural crops derived from the root, the stem, the leaf, or the fruit? Explain.

42. Roots are confined almost entirely to land plants. Explain.

43. Give an example of a root which serves as a store-house for a large amount of food.

44. What advantage has the root over the stem as a place for food storage?

45. Name ten cultivated plants in which the root is the organ useful to man.

46. Name a few plants in which the stem is very much reduced. Under what important disadvantage are such plants?

47. Name ten cultivated plants in which the stem is the organ useful to man.

48. The blade of an ordinary leaf is broad and thin. Explain the advantage of this to the plant.

49. Name ten cultivated plants in which the leaf is the organ useful to man.

50. What makes reproduction necessary among plants and animals?

51. Name ten cultivated plants in which the fruit or seed is the organ useful to man.

52. What important resemblances are there between the physiology of a typical plant and of a typical animal? What important physiological differences are there between these two groups of organisms?

REFERENCE PROBLEMS

9. Are there more species of plants or of animals on the earth today?

10. Are there any plants which lack roots? which lack leaves? which lack a stem? which lack reproductive organs?

11. Give the derivation of each of the following terms and explain in what way it is an appropriate one:

Thallophyte Bryophyte Pteridophyte
Spermatophyte

CHAPTER III

THE SOIL AND ITS IMPORTANCE TO PLANTS

It is impossible to study the plant as a living organism without an understanding of the surroundings or *environment* in which it grows. For most of the Seed Plants, the physical environment may be divided roughly into the *soil* and the *atmosphere*. Of these two, the soil is much the more complex—physically, chemically, and biologically. This fact, together with the profound effect produced upon the plant by changes within it,

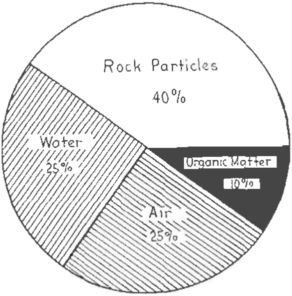


FIG. 11.—Composition of soil. Graph showing the percentage composition, by volume, of a rich, loam soil.

warrants us in devoting to the soil a brief preliminary discussion before we consider in detail the structures and functions of the plant itself.

The soil has three main uses in the plant's economy: It provides an anchorage and support whereby the plant may be held firmly in position; it furnishes the supply of water which the plant uses, and it contributes certain mineral salts essential to the plant's successful activity.

Soils vary much in physical texture, chemical composition, depth, origin, richness, and other respects, but all are normally made up of a mixture of distinct components, each of which has its particular influence upon the life of plants. These components are rock-particles, water, air, humus, dissolved substances, and organisms (Fig. 11).

COIMBATORE

Rock Particles.—The bulk and the basic material of a soil is composed of small, angular particles which have been formed by disintegration of rock. These make up 90 per cent of the weight of ordinary good soil, furnish the necessary anchorage for the plant, and, through the substances dissolved from their surfaces, contribute to the supply of available nutrient materials. The particles vary greatly in size, from those of fine clay to those of coarse gravel. They also differ in shape and in chemical composition according to the type of rock producing them. The irregularity of contour which these particles display makes it impossible for them to fit very closely together, and a considerable amount of space (pore-space) is thus left between them which may be occupied by air or by water. In soils which are in good condition for the growth of ordinary plants the particles cohere in groups to form *crumbs* or *floccules* (Fig. 12), the component grains of which are held together by water-films or by such a cementing substance as clay. One important purpose of tillage is to impart this crumb structure or *flocculation* to a soil. At the soil surface, by the direct action of the rain or by other means, these crumbs may be broken into their constituent particles, which then pack closely together and on drying harden into a firm, clay-like crust.

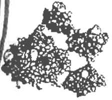


FIG. 12.—Soil-crumbs or floccules. Much enlarged.

Water.—Water is of vital importance to plants in many ways. It constitutes the great bulk of their bodily material; it enters into the manufacture of food; it assists in maintaining the plumpness and rigidity of the tissues; and, in its capacity as a solvent, it serves as the general medium in which most physiological processes are carried on.

The chief source of soil water, and in most cases the only one, is the rain which falls upon the soil surface. Various fates await this water (Fig. 13). A considerable part of it may not enter the soil at all if the surface is hard or the rainfall heavy, but may drain away instead. This *run-off* is lost to plants, and

may even do much harm by washing away a portion of the soil itself. The water which does enter the soil may either *percolate* downward between the particles under the influence of gravity, or may be held in the soil by *capillarity*.

Percolating or *gravitational* water passes downward rapidly if the soil particles are coarse, more slowly if they are finer, until it arrives at a level where all the soil spaces are filled with standing

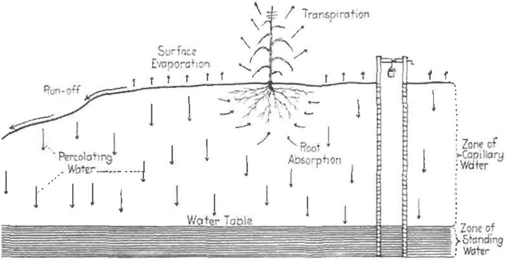


FIG. 13.—The various fates of rain-water which falls upon the soil. It may run off without entering the soil; it may be evaporated from the surface; it may enter the roots and be transpired from the leaves; it may be held in the soil by capillarity, or it may percolate downward to the water-table.

or *hydrostatic* water. This level is known as the *water-table*. Its position at any given point determines the height at which water will stand in a well dug at that point, and its distance below the surface varies from place to place and is subject to much fluctuation. A similar saturated condition occurs in the upper soil layers after heavy rains, but persists there for only a short time. When water has percolated downward to this level it is often beyond the reach of roots, and is thus quite unavailable to plants.

Capillary water is water held in the soil by the force of capillarity. Common observation teaches that when an object (such as one's hand) is immersed in water and then lifted out again, some water still adheres to its surface in a thin film, or "wets" the object. This is due to the fact that there is greater attraction between the surface of the object and the water than is exerted by the force of gravity or the cohesion of the water particles themselves. Any material with a large amount of

surface, internal or external, which may be wetted (such as a sponge, blotting paper or coarse fabric) will therefore hold within *itself, when thoroughly soaked, a great amount of water which* will not drain out under gravity. For exactly the same reason, much of the water entering a soil will fail to percolate through it but will instead adhere in thin films to the surfaces, very great in total area, which are presented by the multitude of soil particles. If the amount of rainfall is small, all of it may thus be retained

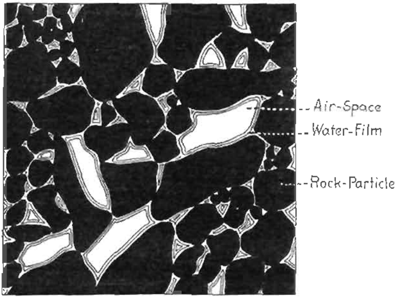


FIG. 14.—Section through soil, much enlarged. A, capillary water-film surrounds each particle and fills the narrow spaces between particles. The larger spaces are occupied by air. Much enlarged.

and none lost through percolation. Each particle in such a moist soil is covered by a thin layer of water (Fig. 14). The films about adjacent particles coalesce, filling the minuter spaces and lining those that are larger, and a continuous film-system is thus set up. It is this *film* or *capillary* water which furnishes plants with the great bulk of their water-supply. One of the important objects in manipulating a soil is to increase, by one means or other, this *water-holding capacity*, and thus to prevent waste through run-off or percolation.

The principle of capillarity is of further importance in determining all movements of water in the soil other than the downward one due to gravity. The familiar fact that when a narrow glass tube is placed in water, the water will rise inside the tube to a point somewhat higher than its level outside, is due to the attraction between the surface of the glass and the water, an

attraction which is sufficient to lift water against gravity. The lifting force will be proportional to the exposed surface of the tube, and therefore where the volume of water is small in relation to this surface (as is the case inside the tube) the water will rise somewhat before the weight of the lifted column counterbalances the pull exerted by the surface attraction. Obviously, the narrower the tube, the higher the column of water will rise, since the volume of liquid to be lifted will be smaller in proportion to the area of the attracting surface. Thus, in any material the

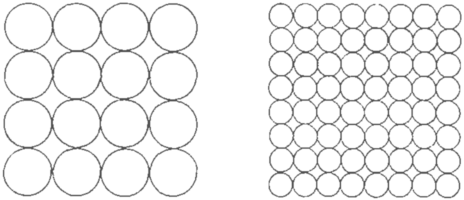


FIG. 15.—The relation between the size of soil particles and the amount of surface which they present. Diagrams of sections through equal volumes of small spheres and of large spheres. The total surface is evidently greater where the size of the particles is less.

structure of which presents a great amount of surface surrounding small but communicating tubes, pores or other narrow spaces, as in blotting paper, lamp-wicks, and the like, water will evidently be carried to a considerable distance in all directions by capillarity. Just such a material as this is the soil. The multitude of its tiny particles, packed closely together, form a capillary system which is able to carry water far. This water tends to surround each particle in a thin, capillary film, but if the soil particles are very coarse the film cannot pass around them, and under such conditions the ascent of water necessarily stops. Water moves readily within the films and when those at the top of the ascending column are thinned through evaporation or through the attraction exerted by still higher and unwetted surfaces, the films below are drawn upon, and water passes upward through the whole system. This movement continues until the weight of the water lifted balances the surface attraction at the top of the column. The height to which water will rise by capil-

iarity is dependent chiefly on the size of the soil particles; for the smaller the particles, the larger will be their surface in proportion to the spaces between them (Fig. 15), and thus the higher will be the rise of water (Fig. 16). In ordinary soil this rise varies roughly from two to twenty feet. It is evident, therefore, that water which has percolated very far below the surface ordinarily cannot be made available to plants again through capillary ascent.

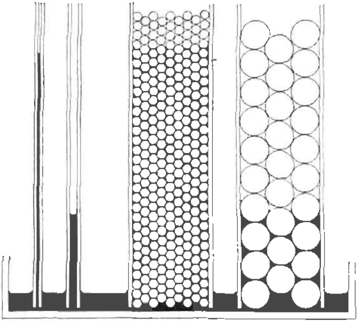


FIG. 16.—Rise of water by capillarity. In the two glass tubes at the left, the rise of water is much higher in the narrower than in the wider one. In the two chambers at the right, which are filled with spheres, the rise of water is much higher where the spheres are smaller.

In most soils there is a capillary movement of water toward the soil surface, where it evaporates. If the particles at the surface are very close together, as they are where the soil has been packed down or where a crust has been formed, a very efficient capillary system is produced there which connects the soil surface with the deeper water-holding layers, and thus greatly hastens the loss of water by drawing it up to a point where it may be evaporated (Fig. 17). An important purpose of tillage is to prevent such waste of water by breaking up the capillary system at the surface and forming there a layer of loose, coarse material called a *mulch*.

Capillary movement of water is by no means always vertical but may take place in all directions within a soil, just as ink spreads in all directions in a piece of blotting paper. This move-

ment tends to continue until the water films are of equal thickness throughout the entire soil mass, causing it to be uniformly moist. When water is removed at any particular point, as by surface evaporation or root absorption, it is therefore drawn thither from all other points until equilibrium is restored.

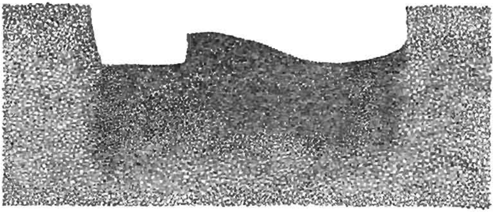


FIG. 17.—A foot-print in loose soil. A vertical slice through the soil under and near a foot-print, showing how the particles which were under the foot have been pressed together. This establishes a better capillary connection with the lower soil layers and causes a more rapid movement of water to the surface, thus often making the foot-print moist while the soil surface around it is dry.

In soils which have lost all their capillary water by evaporation, there still remains around each particle an exceedingly thin film of *hygroscopic* water, which clings so tenaciously that it may be driven off only by subjecting the soil to a high temperature. When the air is very dry, this water is present in minimum amount, but when humidity rises, more water may be taken up directly from the air, or *hygroscopically*. This type of water is removed with such difficulty from the soil particles, however, that the plant is able to obtain little or none of it.

Air.—Since oxygen is essential for the healthy growth of ordinary plant roots, the presence in the soil of a plentiful supply of air is a matter of vital importance. If the spaces between the soil particles become filled with water, most of the air is necessarily driven out, and when this condition of saturation is long maintained, ordinary plants suffer. We have seen, however, that such excess of water normally passes downward by percolation, and as it does so the soil spaces fill again with air. In most cultivated soils, from 20 to 35 per cent of the volume consists of air spaces. The composition of the air which fills these is often somewhat different from that of the atmosphere, the proportion of carbon

dioxide being relatively high. Plowing tends to increase greatly the air content of a soil, since the structure of the whole mass is loosened and the crumbs are more widely separated. A soil in this condition is said to be in good *tilth*. Where water occurs only in capillary form much air is present in the larger spaces, and such a state of the soil is therefore clearly the most favorable for plant growth since then, and then only, is a plentiful supply of water combined with a plentiful supply of oxygen.

Organic Matter.—All rich soils contain a considerable amount of material derived from the dead bodies of organisms, particularly of plants. Roots which die and remain in the soil, and leaves and other plant parts which fall on the soil surface, are the sources from which this organic matter is mainly derived in nature. In the practice of agriculture it is increased in amount by various artificial means. After entering the soil it soon begins to undergo decomposition, and for the most part is finally broken down into simple end-products—carbon dioxide, water, and ammonia. As this organic material decays it becomes characteristically dark in color and undergoes a series of complex chemical changes. In this condition it is known by the general name of *humus*.

Humus is of importance to plants in many ways. It improves the physical condition of the soil, for because of its coarse and fragmentary character it tends to separate the particles and thus to increase materially the air-content of the soil. Since humus absorbs water readily, its presence also adds to a soil's water-holding capacity. The decomposition of humus liberates certain nutrient materials, notably an abundant supply of nitrogen compounds, which ultimately become available to plants. Humus is also the seat and food-supply of the soil bacteria, minute organisms which are indispensable in plant nutrition. Any treatment of the soil which will increase its humus content will therefore tend to increase its productivity, and whatever decreases the humus content will impoverish the soil.

Dissolved Substances.—Soil water is by no means pure water but carries dissolved within it a great variety of substances. *Anything which is to be taken in by the roots of plants must be in solution*, and it is consequently obvious that these dissolved substances are the only portion of the soil, aside from water itself, which is directly available as nutrient material for plants. Their origin and chemical composition are therefore of much importance botanically.

The solvent power of soil water is increased by the presence within it of carbon dioxide, liberated in the respiration of plant roots and of the lower organisms. Thus reinforced, water not only attacks the surfaces of the rock particles but absorbs any soluble material which may appear in the humus or as a product of bacterial activity.

There is a great variety of substances present in the soil solution, and we know from chemical analyses of the ash* of plants that very many of them may be taken into the plant body. Compounds of nitrogen, sodium, potassium, calcium, magnesium, iron, manganese, aluminum, phosphorus, sulphur, chlorine, and silicon are commonly absorbed by the roots, and many others may be taken up occasionally. Certain of these elements are far more important to the plant than others, however, and it has been clearly proven by experiment that seven are essential for normal plant growth: Sulphur, phosphorus, calcium, magnesium, potassium, iron, and nitrogen. The actual amount of these mineral nutrients taken up by the plant is exceedingly small in proportion to the size of the plant body, but in the activities of protoplasm each plays a very necessary part, and a soil which is deficient in any one of them will be unable to support vegetation successfully.

The removal of large amounts of nutrient materials from agricultural soils, in the form of crops and in other ways, reduces the available supply of certain chemical elements, notably nitrogen, phosphorus, and potassium, to such an extent that a fresh supply must be returned to the soil if abundant plant growth is to be maintained permanently thereon. This necessitates the common practice of adding to the soil various types of fertilizers which renew the supply of essential salts there available to plants.

Organisms.—Aside from its service as a medium for the root-growth of higher plants, the soil provides a dwelling-place for a great variety of other organisms, whose activities have a profound effect on the composition of the soil and on the processes which go on therein. Rodents, insects, and angleworms all modify the physical character of the soil by their abode within it. Those most minute and lowly of living things, however, which we group together as *micro-organisms* are of far greater importance,

* The *ash* of plants is the residue left after complete combustion of the plant tissues, and an analysis of it indicates the amount and character of mineral substances present in the plant.

for experiment has shown that without their presence the soil would soon become unfit to support a vegetation of higher plants.

Most notable among these micro-organisms are the *Bacteria* (Fig. 18), tiny, single-celled plants which lack the green pigment chlorophyll. Many of these—the bacteria of decay—decompose the complex organic substances found in humus into such simple end-products as carbon dioxide, water, and ammonia, thus releasing great quantities of nutrient materials which would otherwise be locked up and useless in dead bodies of animals

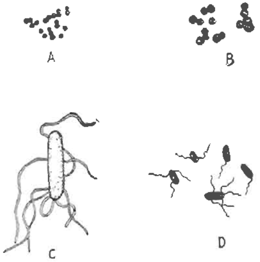


FIG. 18.—Some important soil bacteria. *A*, nitrite bacteria, *Nitromonas;* × 2000. *B*, nitrate bacteria, *Nitrobacter;* × 2000 *C*, a common decay-producing organism, *Bacterium mycoides;* × 1500. *D*, nitrogen-fixing bacteria, *Rhizobium leguminosarum;* × 750.

and plants. Still other bacteria in the soil cause chemical changes of various sorts there, the results of which are of great moment to the higher plants. Notable among these are bacteria concerned with the transformations of nitrogen and its compounds, for through their activity alone is the available supply of this necessary element maintained in the soil. The continual circulation of nitrogen through its various successive stations in organisms, air, and soil is known as the *Nitrogen Cycle* (Fig. 19). Complex nitrogenous substances returned to the soil in the bodies of dead animals and plants are broken down by the bacteria of decay into simpler compounds, which are finally reduced to ammonia. Since most plants can use nitrogen only when it occurs in the form of nitrate salts, however, this ammonia is not directly available to them but must first be converted into nitrate salts through the process of *nitrification.* This is carried on by

two types of nitrifying bacteria; the *nitrite* bacteria, which change ammonia to nitrites, and the *nitrate* bacteria, which in turn convert nitrites into nitrates. In this form nitrogen is readily absorbed and assimilated by plants, and is ultimately returned to the soil again in the bodies of plants or animals, thus completing the cycle. Through the activity of another group of these

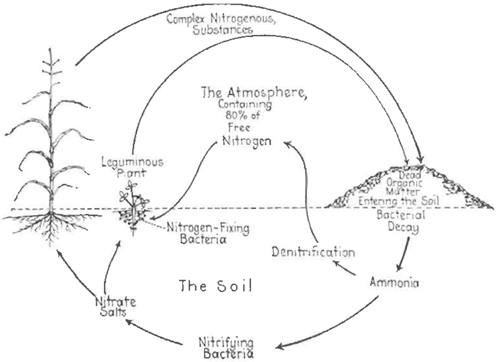


FIG. 19.—The Nitrogen Cycle.

minute organisms, certain of the seed plants are also able to take advantage of the enormous supply of nitrogen in the atmosphere, which is ordinarily quite unavailable. These are the *nitrogen-fixing* bacteria. They are present in most soils and cause the development of the tubercles or nodules usually found on the roots of plants belonging to the Legume family (Fig. 20), which includes beans, peas, clover, alfalfa, and similar plants. These bacteria are able to absorb the free gaseous nitrogen of the air and to build it into nitrogenous compounds in their bodies, whence it ultimately becomes available to the particular plant on the roots of which the bacteria grew. Without drawing at all upon the nitrogen compounds in the soil, a leguminous plant is consequently able to acquire an abundant supply of this important element.

In the case of many species of plants, particularly those which grow in forests or other situations rich in humus, thread-like filaments of fungi are intimately associated with the smaller roots, entering their outer tissues and surrounding the root with a web-like jacket of fungus threads. These very largely take the place of root-hairs and aid the plant in absorbing water and

FIG. 20.—Root tubercles. A part of the root system of a leguminous plant, showing the characteristic tubercles upon the roots, caused by the presence of nitrogen-fixing bacteria.

nutrient material from the soil; and the fungus, as well, is evidently benefited by such relationship. This root-fungus association is known as a *mycorrhiza*. Certain plants have become so dependent in this way upon particular species of fungi that they cannot thrive when these fungi are absent.

In conclusion, we may emphasize again the extreme complexity of the soil and the vital significance to plants of its composition and of the changes which go on within it. The study of this remarkable material has required the collaboration of almost

all of the sciences, but we still lack a precise knowledge of many of its aspects and fail to understand clearly the manner in which it affects the life of plants growing in it.

QUESTIONS FOR THOUGHT AND DISCUSSION

53. Through what processes does bare rock gradually become covered with soil?

54. *Is soil always formed by the rock lying directly under it?* What was the origin of the soil in this region?

55. In what various ways is soil being impoverished or "used up"?

56. In what various ways is soil being replenished?

57. What is the surface of a bit of gravel which is in the form of a solid cube, the sides of which are 1 cm. long? What would be the surface of this bit of gravel if the cube were cut up into smaller cubes with sides of 1 mm. each? What conclusion can you draw from this as to the importance of the size of soil-particles?

58. What disadvantages to plants are there in a soil where the particles are very small? What disadvantages where they are large and coarse?

59. Why are soils in which the particles are small usually more productive than soils in which the particles are large?

60. It is important to have the soil very loose and "mellow" if such "root-crops" as potatoes, carrots, beets, and turnips are to yield heavily. Explain.

61. The surface of land after plowing is a few inches higher than it is before plowing. Why?

62. In what respect is the cutting off of forests bad for the soil?

63. Is a gentle shower or a hard, beating rain better for the soil and for plants growing thereon? Explain.

64. It is harmful to the soil to till (or "work") it immediately after a rain or while the soil is very wet. Why?

65. Why is extensive removal of forests in a region often followed by floods there?

66. What various means of soil treatment can you suggest for insuring that the largest possible proportion of the rainfall is utilized by plants growing on this soil?

67. Which will absorb and hold a larger amount of water: Clay or sand? Why?

68. Will the rise of water by capillarity be higher in sand or in clay? Why?

69. Which is better for plant growth in a dry season, a clay soil or a sandy one? Why?

70. A layer of coarse gravel a few feet below the surface of the soil makes the soil above it much drier than similar soil not underlain by gravel. Why?

71. Why does the surface of soil which has been perfectly dry during the day often turn moist at night?

72. Why is the surface of the soil in arid regions often caked with a crust of salts?

73. Why is a well-forested region apt to suffer less from drought than one with no forests?

74. Which will generally be colder, a soil with fine particles or one with coarse? Why?

75. A potted plant will dry out the soil in its pot very uniformly. Explain.

76. Is it better to water house plants by pouring water over the soil or by letting the pots stand in water for a little while? Why?

77. Explain *exactly why* a mulch on the soil surface reduces loss of water from the soil through evaporation.

78. What basis in fact is there for the saying, "Water your garden with a rake"?

79. Why is it advisable to scratch over a garden with hoe or rake as soon after a rain as the soil is workable?

80. Why is it advisable to plow as early in the spring as the soil is workable?

81. Why is it important to water a plant before it is transplanted?

82. Give three reasons for pressing the soil firmly about the roots of a plant after it has been transplanted.

83. After a plant has been transplanted, it is well to scratch over the ground around it with a hoe or rake. Why?

84. What advantage is gained by pressing down the soil above seeds after planting them?

85. After sowing seed for certain crops, a farmer often rolls the soil with a heavy roller. What is gained by this?

86. Why is irrigation necessary in some regions but not in others?

87. What is the best time of day to water a garden? Why?

88. Why is it necessary to drain wet land before ordinary crops can be grown thereon?

89. In what ways is the air in the soil constantly being changed and renewed?

90. Of what use is the air in the soil in addition to providing oxygen for plant roots?

91. Give two reasons why the formation of a "crust" on the soil surface is harmful to plants.

92. Is it better to water house plants frequently and lightly or infrequently and heavily? Why?

93. How is the supply of humus maintained in soils which are not under cultivation?

94. Dark-colored soil is usually richer than light-colored soil. Explain.

95. Why is soil from low land usually darker in color than soil from a side hill?

96. The continual addition to the soil of no other fertilizer than the ordinary "commercial" fertilizers is generally found to be harmful. Why?

97. What conditions are there under which the addition of humus to the soil might be actually injurious to plants?

98. How would you prove that a particular element is, or is not, essential to plant life?

99. Most commercial fertilizers contain nitrates, phosphoric acid, and potash. Why?

100. A good crop of corn, wheat or potatoes removes about 50 pounds of nitrogen per acre from the soil. Nitrogen composes about four-fifths of the weight of the atmosphere. At this rate of removal by crops, how many years would the nitrogen in the air over an acre last, provided that it could be made available to the plants growing there?

101. Name several ways in which chemical substances essential to plant growth are wasted in modern civilization. What methods can you suggest to prevent some of this waste?

102. Why are wood ashes so valuable as fertilizer?

103. Why do sewers often become clogged with roots?

104. What two important contributions to human welfare are made by the bacteria of decay?

105. What various organisms living in the soil may be harmful to plants?

106. What is the chief importance of angleworms in the growth of plants?

107. Plants native to the woods will often fail to thrive when transplanted to a garden, even though the soil there is rich and the conditions of shade and temperature are much like those in the forest. Can you suggest a reason for this difficulty?

108. At what point in the nitrogen cycle, and in what form, is loss of available nitrogen most apt to occur?

109. Manure left freely exposed to the air will lose much of its fertilizing value. Why?

110. For many plants, rather old manure is better than that which is absolutely fresh. What reason can you suggest for this?

111. Plants which have very deep roots (such as certain weeds and cover-crop plants) are sometimes of advantage to crops which are subsequently grown on the soil. Why?

112. A "cover-crop" is a crop (such as rye) planted in late summer or early fall which grows up enough to cover the ground before winter. What are the advantages of planting such a crop?

113. Why is flood-plain or "river-bottom" soil usually very productive?

114. In what ways may the productivity of a soil be diminished other than by the removal of crops grown upon it?

115. It has long been recognized that land which is left uncropped or "fallow" for a few years will prove to be more productive afterward. How do you explain this?

116. In what ways is the productivity of a soil maintained in nature, before it becomes the seat of agriculture?

117. What other functions may the addition of fertilizer to the soil perform aside from that of providing nutrient materials for plants?

118. State at least three advantages which are gained by plowing the soil.

119. Cultivating the soil around growing crop plants (by hoeing or otherwise) is not necessary or advantageous after the crop has covered the ground fairly *well*. Explain.

120. How can soil in a state of nature, entirely without cultivation, support plant life so well?

121. Give several reasons for the desirability of keeping the soil around a young fruit tree well "mulched."

122. Vegetable growers often sterilize by steam, formalin or other means, the soil in the greenhouse beds where they are to grow their young plants for later transplanting outside. What advantages has *this process? What disadvantages would it have if applied in the* field?

123. Farmers sometimes build a big bonfire over the spot where they are going to start their young plants of cabbage, tomato, and similar crops. What two advantages are gained by this?

REFERENCE PROBLEMS

12. What is meant by *tillage?*

13. What is *irrigation* and how is it practiced?

14. Soils which are poorly aerated are apt to be "sour." Explain.

15. Distinguish between animal manures, green manures, and commercial fertilizers, and state the advantages in the use of each.

16. What is the chemical formula of atmospheric nitrogen? of ammonia? of potassium nitrate? of some complex nitrogenous compound?

17. May *organic* substances dissolved in the soil solution enter directly into ordinary green plants and be used by them as food? Explain.

18. Give an example of a crop plant which thrives best on alkaline soil; one that thrives best on acid soil. Which of these two soil types do most crop plants favor?

19. About how many bacteria are usually present in 1 c.c. of rich soil?

20. What is "rotation of crops" and what is its value?

21. Give the derivation of each of the following terms and explain in what way it is an appropriate one:

Capillarity	Humus	Mycorrhiza

CHAPTER IV

THE ROOT AND ITS FUNCTIONS

The portion of the plant most intimately related to the soil is the root. This organ has two major functions—to anchor the plant firmly and to absorb water and certain important nutrient materials from the soil. Beyond this, the root often serves as a

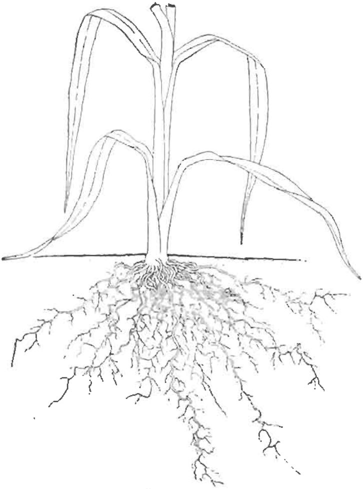


FIG. 21.—A fibrous root-system (Grass). The roots are all rather slender and much branchd.

storage reservoir for food, and may perform various other functions.

External Structure.—The most common type of root is a rather slender and profusely branched structure, penetrating the soil in

all directions and forming a *fibrous* root-system (Fig. 21). Its advantages for anchorage and absorption are obvious. Somewhat less common are types which possess a single main root or *tap-*

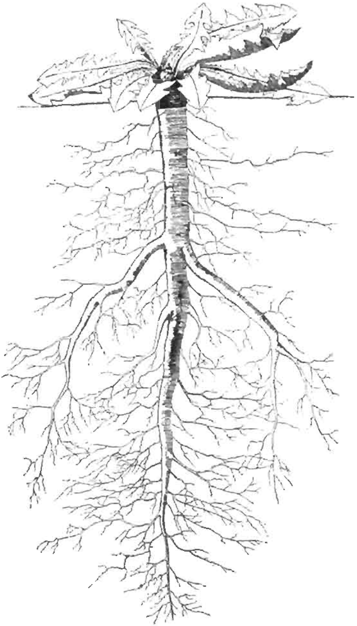


FIG. 22.—A tap-root system (Dandelion). From the tap-root a large number of smaller, lateral roots arise.

root, penetrating deeply into the soil and much stouter than the *lateral roots* which arise from it (Fig. 22). Tap-roots lend themselves readily to storage purposes and frequently become large and fleshy. The root-systems of many plants are intermediate

between these two main types. Others may sometimes depart radically from the normal forms in response to certain special and unusual functions which they have assumed.

The Absorbing Region.—Absorption of water and nutrient material is carried on only by the younger portions of the root, near its tip. The very tip itself is covered with a sheathing *root-*

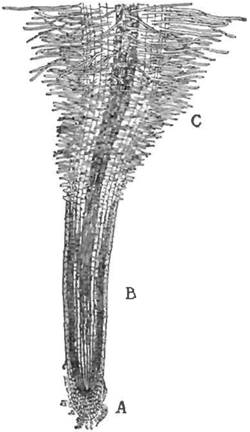


FIG. 23.—Tip of a root, showing root-cap (*A*), growth zone (*B*), and root-hair zone (*C*). *(From Ganong, "Textbook of Botany", copyrighted by the Macmillan Company. Reprinted by permission).*

cap of cells, which protects the delicate underlying tissues as the root pushes its way through the soil (Fig. 71). Back of this is a short region of growth, the only place where elongation of the root occurs. Behind this, in turn, is the absorbing region, a somewhat longer zone the surface of which is covered with thousands of exceedingly delicate filaments, the *root-hairs* (Fig. 23). Each hair is an elongated projection growing out from one of the surface cells of the root (Fig. 24), its sap-cavity and lining of cytoplasm being continuous with those of the root-cell of which it forms a part (Fig. 25). The root-hair may reach a length

of several millimeters and forces its way into the minute crevices of the soil, thus coming into most intimate contact with the soil particles (Fig. 26). Through the enormous surface which these root-hairs expose to the soil, absorption of water and mineral

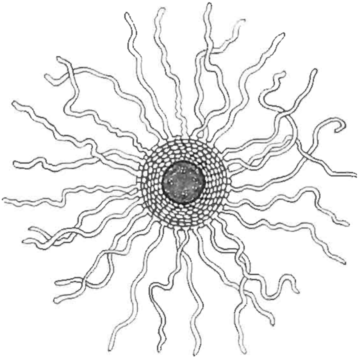


FIG. 24.—Root-hairs and their relation to the root. A transverse section across the root-hair zone, showing the attachment of the hairs. In the root may be distinguished the fibro-vascular cylinder (in the center), surrounded by the cortex.

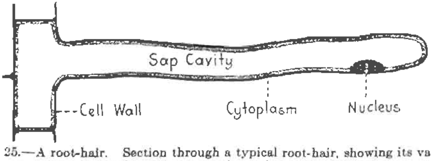


FIG. 25.—A root-hair. Section through a typical root-hair, showing its various structures and its relation to the surface cells of the root.

salts takes place. Root-hairs are generally short-lived, dying away as the corky bark begins to appear. A root-hair zone of fairly constant length thus follows behind the growing root-tip, new hairs appearing in its younger portion to replace the oldest ones, which are continually dying away.

The Plant Cell.—The root-hair (including its basal portion) is a plant *cell*. Since a knowledge of the structure and functions of cells is obviously essential if we are to understand how the root-hair is constructed and does its work, or, indeed, how any other part of the plant is put together and functions, it will be necessary at this point, before we discuss the physiology of the root, to

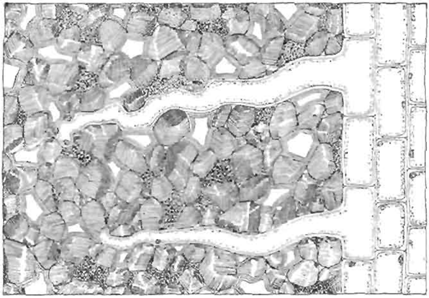


FIG. 26.—Diagrammatic section through a portion of a young root and the adjacent soil, showing two root-hairs forcing their way between the soil particles. Rock particles, water films, and air spaces in the soil are shown. Much enlarged.

describe briefly some of the more important characteristics of cells in general and of plant cells in particular.

We have already spoken of that remarkable living material which is called *protoplasm*, the seat of all the various activities which are maintained in animals and plants, and the only portion of their bodies which is truly *alive*. Physically, protoplasm is a thin, jelly-like, colloidal substance, but its minute structure is not clearly known. Chemically, it is a mixture of very complex proteins and is thus composed chiefly of carbon, oxygen, hydrogen, and nitrogen. Protoplasm is the "physical basis" of all life and the most extraordinary material known to man.

The protoplasm of the plant body is not a directly continuous mass but is broken up into minute parts, the *cells* or *protoplasts*, each of which is a distinct and more or less independent unit, possessing a definite structure and carrying on within itself a variety of physiological processes (Fig. 27). Around the cell the protoplasm secretes a dead *cell-wall* composed of the characteristic

plant substance *cellulose*. This is firm in texture but easily penetrated by water. The protoplasm of the cell has two distinct portions—the *nucleus*, a dense, somewhat spherical body which appears to be the directive center for the cell's activities; and the *cytoplasm*, thinner and more watery in texture, which lines the inner surface of the wall in a tenuous layer and is bounded,

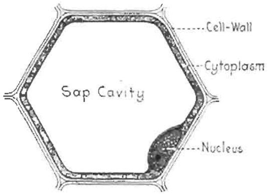


FIG. 27.—A typical plant cell. Diagrammatic drawing showing the central sap-cavity, surrounded by a layer of cytoplasm which lines the cell-wall. Embedded in the cytoplasm is the nucleus. Parts of the cell-walls of six adjacent cells are also shown.

without and within, by a very delicate membrane. Embedded in the cytoplasm frequently appear small, somewhat denser bodies, the *plastids*. These perform special functions, such as carrying on the manufacture of food, building up starch-grains or producing colors. In many cases it has been shown that the cytoplasm is not passive and immobile, but that within it a slow, streaming movement often takes place. In mature cells, the entire central portion of the cell is occupied by a *sap-cavity* or *vacuole*, filled with water in which various substances are dissolved, and surrounded externally by the layer of cytoplasm. A typical plant cell may thus perhaps be likened roughly to an inflated football or basketball, the firm leathery covering corresponding to the cell-wall; the thin inner bladder of rubber, tightly pressed against it, to the layer of cytoplasm; and the air-space to the sap-cavity. A comparison to an automobile tire, with its stout shoe or casing, its delicate inner tube, and its central air-cavity, might also be made.

Cells are normally very small objects, averaging about .01 mm. in diameter, and varying widely in shape and character according to the function which each performs, whether this be support, absorption, conduction, storage, protection, food-manu-

facture, growth, or reproduction. The plant body is composed of a multitude of cells, bound firmly together by cementing substances to form an entire, coherent organism. As we consider the various tissues and organs in detail, we shall have occasion to describe the particular characteristics which their cells display.

Internal Structure of Roots.—Internally, roots show a very marked structural differentiation. In a young root, three main cell-systems or tissues are distinguishable—the *epidermis*, the *cortex*, and the *fibro-vascular* cylinder (Fig. 28).

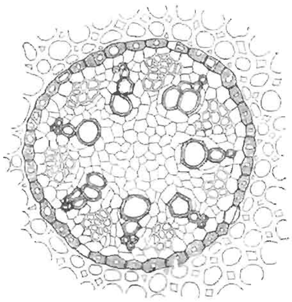


FIG. 28.—Transverse section of the fibro-vascular cylinder of a young root. *The bundles of thick-walled wood cells alternate with bundles of thin-walled* bast cells. The whole is surrounded by an endodermis, outside of which is the cortex of the root. (*From De Bary*).

The epidermis of the root, like that of all other plant organs, is a single layer of cells in thickness. These cells are normally protective in function, but in the root-hair zone many of them produce on their outer surface a characteristic projection, the root-hair itself.

The cortex lies just under the epidermis and is of varying thickness. In the young root, its cells serve to transmit water and dissolved substances from root-hair to fibro-vascular cylinder, and, in the older roots, to store food. Most of the fleshy portion of storage-roots consists of enlarged cortex. The innermost layer of cortical cells is often especially modified and is then known as the *endodermis*.

The fibro-vascular cylinder occupies the core of the root, furnishing mechanical strength and serving as a highway for conduction. As in other organs of the plant, it is composed of two main tissues, the *wood* or *xylem* and the *bast* or *phloem*. The wood, which forms the central axis of this cylinder, is usually star-shaped in cross section and is composed for the most part of thick-walled and much elongated dead cells, the walls of which have become woody. It provides rigidity for the root and conducts upward the water and dissolved substances which

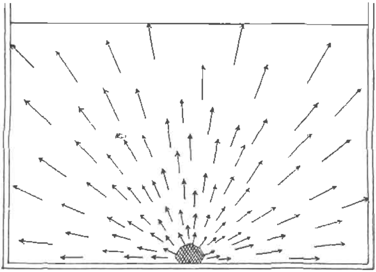


FIG. 29.—Diffusion of a dissolved substance. Diagram representing the outward diffusion of molecules which are being dissolved from the surface of a soluble substance immersed in water.

enter from the soil. Between the points of the star are patches of bast, formed of thin-walled cells which transport manufactured food upward or downward.

In older roots the fibro-vascular cylinder, particularly as to its woody portion, increases greatly in thickness through the activity of a growing zone or *cambium*, just as does the stem; and a corky bark is usually developed on the outside.

Diffusion and Osmosis.—The most important function of the root is to absorb from the soil the water and mineral substances needed for the plant's life and growth. This involves the physical processes of *diffusion* and *osmosis*, a consideration of which is necessary before we can understand clearly this primary activity of the root.

Diffusion.—Diffusion may be defined as the tendency of any substance, when it occurs as a gas or in solution, to become

evenly distributed throughout the whole space available to it by moving from points of greater to points of lesser concentration. Its operation is familiar in the diffusion of odors, for the minute particles given off by any strongly scented substance will move outward rapidly, even in perfectly still air, and will soon become equally distinguishable in all directions from their point of origin. Two gases liberated within a closed space soon diffuse throughout its whole extent and become thoroughly mixed. In the same way, a crystal of salt dissolved in a vessel of water will in time have its molecules dispersed so uniformly, even though the liquid is free from moving currents, that samples taken from any part of the contents of the vessel will be salt solutions of exactly the same strength (Fig. 29). This constant tendency toward diffusion is explained by the fact that in gases and liquids the molecules are in very active movement, continually striking against one another and rebounding. There are obviously fewest collisions, and thus most frequent opportunity for unobstructed movement, in those directions where there are fewest molecules, and in such directions a dispersal of the molecules therefore necessarily takes place until they are present everywhere in uniform abundance. The principle of diffusion is operative in so many of the physiological processes of plants that it must be thoroughly grasped if these processes are to be understood.

When two liquids are separated by a membrane through which they can pass, diffusion between them will still take place. Such diffusion through a membrane is called *osmosis*, and it tends to continue (if the permeability of the membrane allows) until the composition of the liquids on both sides of the membrane is the same. If a solution of salt in water, for example, is present on one side and pure water on the other, the salt will tend to diffuse through the membrane until its concentration is the same throughout. It is important to note that the *concentration* (the amount of substance dissolved per unit of volume) rather than the total amount of the substance or the bulk of the solution, is the factor which determines the direction and rate of diffusion. It is by diffusion through the cytoplasmic membranes of the root-hair that mineral salts in the soil solution enter the plant. This inward movement of any given salt will continue so long as its concentration is greater in the soil water than in the sap of the root-hair.

Osmotic Movement of Solvents.—This phenomenon of osmosis is complicated, however, by the fact that the dissolving liquid or *solvent* (water in this case) as well as the dissolved substance will pass through the membrane, and by the remarkable circumstance that where such movement occurs, it is always more rapid in one direction than in the other. Experiment has shown that if two solutions of different concentrations (or a solution and pure water) are separated by a membrane, *a movement of water takes place from the less concentrated to the more concentrated solution*, and tends to continue till both are of the same concentration; and that the rate of this movement is proportional to the difference in concentration. The more concentrated solution will therefore tend to expand through this access of water, and, if it is confined within a closed space, a pressure, often of considerable magnitude, will develop.*

As to why such a movement of water occurs no complete agreement of opinion yet exists, for the process of osmotic interchange involves some of the less clearly understood phenomena of physical chemistry. We may assume that the dissolved substance has an affinity or attractive power for water, and that this attraction increases with the concentration of the substance; or that the molecules of the dissolved substance interfere with the free molecular movement of water molecules, so that where there is little material in solution the water molecules strike the membrane and pass through it oftener than they can where much material is in solution; or we may regard the whole phenomenon as really a manifestation of the fundamental principle of diffusion, since the tendency is for the solutions on both sides of the membrane to become equal in concentration, although this is here brought about by a movement of the dissolving liquid as well as of the dissolved substance itself. None of these explanations is entirely satisfactory, but they may perhaps help to picture the process more clearly to our minds. The essential fact remains that water will pass through a membrane *toward the more concentrated solution*, explain it as we may; and upon this fact depends the power of the plant to withdraw water from the soil.

Permeability of the Membrane.—Thus far, we have assumed that both the dissolved substance and water may pass with per-

* Osmotic phenomena are shown by other solvents than water, but since water is the all-important solvent in physiology, we shall confine our attention only to those osmotic processes in which it is involved.

fect freedom through the membrane, or that the membrane is *permeable* to them. All osmotic membranes are readily permeable to water, but we find that they differ markedly in the ease with which dissolved substances of various sorts can diffuse through them. One membrane may be perfectly permeable to a given substance; another may allow it to pass slowly and with difficulty, and another may exclude it altogether. Nor does even the same membrane display an equal degree of permeability to all substances, for some may pass through it easily, others with difficulty, and others not at all. To what these differences in permeability are due we do not know, but they are presumably caused by the relations between the structure of the membrane and the size and character of the molecules of the dissolved substance.

A membrane which allows water to diffuse through it but does not allow a given dissolved substance to do so is called *semi-permeable,* and it is a highly important biological fact that all membranes in living cells seem to belong to this class. The membrane of a root-hair cell, for example, allows water to pass readily but is impermeable to such substances as sugar, which are dissolved in the sap solution. The cell is thus able not only to retain these valuable materials within itself, unwasted by outward diffusion, but to use them as a permanent means of drawing in osmotically a supply of water from the soil, since their presence within the root-hairs normally maintains the sap of these cells at a higher concentration than the adjacent soil solution. This same membrane, however, is permeable to most of the mineral salts present in the soil, which are thus able to diffuse readily into the root-hair.

Other Principles of Osmotic Action.—Before we attempt to apply the principles of osmosis to the living plant, however, we should fix clearly in mind certain facts with regard to osmotic phenomena in general about which confusion frequently arises. *First,* substances which are not soluble or which for any reason are not in solution *cannot diffuse* and have no osmotic effect whatever. Sugar, for instance, is soluble and is osmotically active, but the moment it is converted into starch, which is an *insoluble substance, it loses its osmotic effect entirely. Second,* the osmotic strength of a solution, and consequently its power to attract water, is determined not by the chemical nature of the dissolved substances but by the total concentration of material,

of whatever kind, which is in solution. A solution of sugar, one of salt, one of a mixture of the two, or one containing half a dozen substances, may all have exactly the same osmotic concentration. *Third*, the diffusion of water through a membrane and the diffusion of salts through the same membrane occur *quite independently of one another*. Water will move through a membrane from a solution of lesser to a solution of greater total concentration, but a dissolved substance, following the general law of diffusion, will pass from a point where that substance is abundant to one where it is scarce, always providing that the membrane is permeable to it. Given the proper conditions, it is quite possible for a dissolved substance to pass through a membrane osmotically with no movement of water taking place at all, or for water to move without a movement of dissolved substances, or even for water to pass in one direction and dissolved substances in the other. *Fourth*, if there is more than one substance in solution, each will tend to diffuse quite independently of all others. Differences in the concentration of each substance, *considered by itself*, are what determine the rate and direction of diffusion of that substance.

Diffusion and Osmosis in the Plant Cell.—It is upon the principles of diffusion and osmosis that the plant depends, not only for the absorption of water and mineral substances from the soil, but for most of the circulation of materials which goes on within the plant body. We have already outlined briefly the structure of a typical plant cell and may now consider the osmotic interchanges which go on therein.

The cell wall in plants is ordinarily composed of cellulose. Like most organic materials, cellulose has the capacity of absorbing water vigorously by *imbibition* and will therefore swell considerably if placed, when dry, in contact with water. This expansive ability of the cell wall is of some value in certain of the plant's activities, as in the germination of the seed, but the wall of an ordinary living cell is moist and has imbibed water to the limit of its capacity. Water, and practically all substances in solution, pass through this cellulose wall with great readiness, and since it thus offers practically no resistance to diffusion, its osmotic effect is slight.

We have noted that, in the mature plant cell, the cytoplasm is dispersed in a thin layer closely pressed against the inner surface of the cell-wall, and that it completely surrounds a large central

vacuole or sap-cavity, filled with water in which various substances, sugar usually prominent among them, are dissolved. On its outer surface next the wall, and on its inner surface next the sap-cavity, the cytoplasm is bounded by a delicate membrane, so that we find here fulfilled all conditions necessary for osmotic activity—one solution, in the sap-cavity, separated by a membrane or membranes from another solution, which may be the soil water (in the case of a root-hair) or the sap-solution of an adjacent cell.

These cytoplasmic membranes, unlike the cell-wall, offer resistance to the diffusion of certain things and are thus highly important in cell physiology. We find that they are characteristically semi-permeable, preventing the passage of such substances as sugar, which are dissolved in the sap-cavity; and we have already noted that the cell is thus able to retain these valuable materials within itself and to use them as a means for bringing in osmotically a continuous supply of water from the soil or from adjacent cells. To the essential mineral salts and to many other dissolved substances, however, these membranes are generally permeable, though in varying degrees, and the cell is therefore readily able to absorb a supply of such substances from any adjacent solution. It has been found by experiment that the degree of permeability of the cell membranes is not a fixed and constant one but is subject to change from moment to moment in response to changes in the environment or in the protoplasm itself. A cell which at one time admits a given substance very readily may at another allow it to enter but slowly, or may exclude it altogether. Many of the physiological activities of the cell are probably regulated by changes in the permeability of its membranes.

The rapidity with which a substance passes through a membrane is due not only to these differences in permeability but to differences in the concentration of the solutions on the two sides of the membrane. Where this difference is great (other things being equal) osmotic diffusion will be more rapid than where it is slight. Therefore if the concentration of a dissolved substance within a cell is reduced, either by its diffusion into an adjacent cell or its conversion into an insoluble form (as must occur when it enters into the construction of a complex organic molecule in the protoplasm) the rate at which a new supply enters the cell from without is at once correspondingly increased; but the

moment its concentration becomes equal, within and without the cell, the movement of this particular substance ceases, even though others are passing rapidly through the membranes.

The Absorption of Water and Salts.—This activity of the cell as an osmotic system evidently controls its most important functions. Let us first consider the role played by osmosis in that process which is the immediate subject of this chapter, the

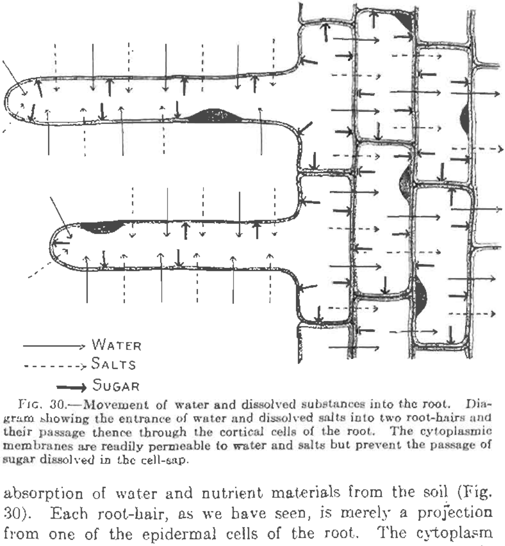


FIG. 30.—Movement of water and dissolved substances into the root. Diagram showing the entrance of water and dissolved salts into two root-hairs and their passage thence through the cortical cells of the root. The cytoplasmic membranes are readily permeable to water and salts but prevent the passage of sugar dissolved in the cell-sap.

absorption of water and nutrient materials from the soil (Fig. 30). Each root-hair, as we have seen, is merely a projection from one of the epidermal cells of the root. The cytoplasm and sap-cavity of the cell extend into the root-hair, the whole of which is thus lined by a thin cytoplasmic layer, with its membranes (Fig. 25). The root-hair penetrates the soil and comes intimately in contact with the soil-particles, to the surface of each of which a thin water-film normally adheres. In this water are dissolved a great variety of substances, but the total concentration of the soil solution is normally less than that in the

sap-cavity of the root-hair, where sugar and other materials are dissolved. In obedience to the law of osmosis, therefore, water will pass from the soil solution through the cytoplasmic membranes of the root-hair and into its sap-cavity. This flow of water will continue so long as there is a difference in total density between soil-solution and sap-solution. Of course if the soil becomes dry and the film around each particle grows so thin that the surface attraction of the particle equals the osmotic attraction of the root-hair solution, the flow will necessarily cease; and if this condition occurs throughout the whole soil mass, the plant will suffer from drought.

Salts and other substances in the soil-solution diffuse through the root-hair membranes quite independently of the passage of water, and the rate at which they enter depends upon the factors which we have above considered. Any substance which is in greater concentration in the cell-sap than in the soil-water, and to which the membranes are permeable, will of course, diffuse outwardly into the soil; but except for carbon dioxide, which is given off in considerable quantities as a product of respiration in the root, there seems to be comparatively little loss of material from the plant in this manner.

As water is taken into the sap-cavity of the root-hair, the solution there becomes less dense; and the first cell of the cortex is consequently able in turn to withdraw water osmotically from the root-hair cell. The second row of cortical cells may now withdraw water from the first, and this process will continue until the water reaches the central cylinder. The water-ducts here, however, are nothing but dead shells, their living cytoplasm having disappeared as soon as the thick cell walls were completed. They are filled with water, and it is hard to understand why water should move into them from the cells of the cortex rather than in the reverse direction. In the innermost layer of cortical cells, a considerable pressure is probably developed by osmosis, and water may simply be squeezed through the cytoplasm and into these ducts. We know, at any rate, that water is forced up through the ducts under a good deal of pressure. This *root-pressure* may be measured by a gauge attached to an opening in the stem. As to what causes water to rise to great heights in the trunks of trees we shall speak later; but root-pressure is apparently only one of the factors involved.

Other Osmotic Phenomena in the Plant.—Not only the absorption of water from the soil, but the whole process of circulation within the plant body, as well, is primarily an osmotic one; for the salts taken in by the root-hairs, and any dissolved substances in other cells throughout the plant, move from cell to cell by diffusion through the cytoplasmic membranes.

Still another contribution of osmosis to the plant's activities lies in maintaining the turgidity of the tissues. It is evident that if a cell has a strong sap-solution and is thus able to absorb water vigorously, it will become plump and fully expanded and will press tightly against its neighbors. If all the cells become turgid in this way the whole plant will tend to be erect and rigid, like an inflated balloon. In the case of parts which do not possess a firm skeleton, such as the leaf blades, floral organs, or other comparatively soft structures, this turgidity is necessary to maintain their form, firmness, and proper functioning. Conversely, if a cell is exposed to a solution of greater concentration than its cell-sap, water will be withdrawn from it, it will collapse, and its cytoplasm will be pulled away from the walls. Such a condition of *plasmolysis*, if extreme or long-continued, will result in the death of the cell; and, if extensive, in the death of the plant.

Osmosis also plays an essential part in growth, for at any growing region we find a point where the cells are multiplying in number but are still small, and another point behind this where each expands rapidly to its final size. This expansion, with the consequent stretching of the cell-walls and growth of the tissues, is due to the rapid absorption of water by the young and delicate cells, the sap of which is rich in dissolved sugar. The force exerted by any growing region is thus primarily due to osmotic pressure.

Other Functions of the Root.—We have briefly discussed the root as an organ of anchorage and of storage, and in more detail as an organ of absorption. It has less frequently certain other functions which should be mentioned here. Roots may arise from almost any part of the stem and sometimes from the leaves. In many climbing plants they are produced abundantly on these aerial organs and serve to hold the plant firmly to its support. In corn, stout roots arise from the stem at a little distance above the ground and pass into the soil, thus acting as props or guy-ropes for the tall plant. In epiphytes, the roots are sent out directly into the air and possess a characteristic spongy envelope

which absorbs and holds rain-water and dew. In parasitic plants the roots are converted into short, sucking organs, penetrating the host-plant and withdrawing therefrom the food upon which the parasite lives.

The root and the leaf are the two most important vegetative organs of the plant, and it is therefore the leaf which we shall next discuss.

QUESTIONS FOR THOUGHT AND DISCUSSION

124. Which is apt to be more regular and symmetrical in shape, the root-system or the stem-system of a plant? Why?

125. In a young plant growing from the seed, the root is larger and better developed at first than the stem or leaves. Explain.

126. Tap-roots are usually tapering in shape, being broadest near the surface of the ground and gradually narrowing below. Explain.

127. Do all roots grow directly downward, provided that there are no obstacles in the way? Give evidence for your answer.

128. It has been found that for most species of plants there is a rather definite distance below the surface of the ground at which the bulk of the roots are formed. Some species are deep-rooted, some shallow, and others intermediate. What physiological differences between the plants can you suggest which might cause these structural differences?

129. Why does the planting of grass on sand-dunes stop the drifting of the sand?

130. Why does a covering of grass turf or other close plant growth prevent the erosion of soil on steep banks and other exposed situations?

131. As a "soil-binder" to prevent erosion would a crop of carrots or a cover of grass be better? Why?

132. If from around a tree which has been growing in the forest all its neighboring trees are cut down, it is then much more likely to blow over than is a tree which has always grown in the open. Why?

133. If a tree-trunk is partly buried, for instance through raising the level of the soil about it by grading or other means, why is the tree likely to die?

134. Which type of plant do you think would withstand a drought better, one with a fibrous root or one with a tap-root? Why?

135. Which do you think will tend to have the deeper root-system, a bog plant or a desert plant? Why?

136. Do you think that a root-system will tend to spread farther in rich soil or in poor soil? Why?

137. Roots will usually grow toward a supply of nutrient material in the soil. Can you suggest what causes them to do this?

138. Root-hairs are entirely absent on the older portions of a root. Why?

139. Root-hairs are absent from the growing region at the tip of the root. Of what advantage is this fact to the plant?

140. Of what advantage are root-hairs to the plant aside from their function in the absorption of water and salts?

141. Root-hairs are commonly absent in water plants. Explain.

142. The fibro-vascular system of the root is usually in the form of a solid rod, and that of the stem in the form of a hollow tube. Of what advantage to the plant are these arrangements of the tissues?

143. Why is the soil immediately around the base of a tree trunk somewhat higher than the adjacent soil?

144. Give an example (other than those cited in the text) of a plant which has a fibrous root-system; a tap-root; climbing roots; parasitic roots.

145. Why is protoplasm regarded as the only really "living" substance in the plant?

146. What are some of the advantages of cellular structure in plants and animals?

147. Give all the reasons you can think of for the fact that cells should be such very small objects.

148. Why do so many cells have a six-sided appearance?

149. Of what advantage is the streaming of protoplasm which commonly takes place in the cell?

150. What important functions does the cell-wall perform?

151. Are there any cells of the plant which are useful to the plant after they die?

152. If a sac made of bladder or a similar osmotic membrane is filled with molasses, tied up, and placed in a vessel of water, what will happen?

153. If this same sac is filled with water, tied up and placed in a vessel of molasses, what will happen?

154. Under what conditions will water pass through a membrane osmotically without any movement of dissolved substances taking place? When would this be likely to happen in the root-hairs of plants? Explain.

155. Under what conditions will a dissolved substance pass through a membrane without any movement of water taking place? When would this be likely to happen in the root-hairs of plants? Explain.

156. Under what conditions will water pass through a membrane in one direction and a dissolved substance in the other? When would this be likely to happen in the root-hairs of plants? Explain.

Note.—Assume in the five following questions that the sac is made of an elastic membrane which is semi-permeable in that it allows the free diffusion of water through it but entirely prevents the passage of sugar. Assume further that this membrane is readily permeable to dissolved salt. Under the conditions set forth in each question, state clearly what will happen, carrying the process through to its conclusion and noting the differences, if any, between early and later stages.

157. What will happen if the sac is filled with a solution of sugar and placed in a vessel of pure water?

158. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is of lesser concentration than the sugar solution in the sac?

159. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is equal in concentration to the sugar solution in the sac?

160. What will happen if the sac is filled with a solution of sugar and the liquid in the vessel is a solution of salt which is greater in concentration than the sugar solution in the sac?

161. What will happen if the sac is filled with a mixture of sugar and salt solutions of equal concentration and that the liquid in the vessel is pure water?

162. Can a plant take out all the water from the soil around its roots? Explain.

163. The stems of most woody plants will "bleed" if cut in the spring, but will not do so if cut in the summer. Explain.

164. Why do tomatoes and other soft and fleshy fruits tend to split open in a wet season?

165. How does it happen that a plant can take up such large amounts of salts when these salts occur in such very weak concentrations in the soil?

166. Many plants thrive for long periods without extending their root-systems into fresh regions of soil. How are they able to obtain an unfailing supply of nutrient salts under these conditions?

167. A plant grown in "water-culture" (in a jar of water containing the necessary nutrient salts in solution) will almost completely remove these salts from the jar, even though its roots fill only a small part of the jar. Explain.

168. Iodine is much more abundant in the tissues of certain seaweeds than it is in the sea water. Explain how this can be.

169. How is it possible for a group of cells in the middle of a tissue, surrounded by other cells, to contain large amounts of a substance which is rare or absent in the other cells?

170. The text states that the cell-membrane of a root-hair is impermeable to sugar, and that sugar therefore cannot get out of the root-hair into the soil. If this is true, how do you think the sugar was able to get into the root-hair in the first place?

171. A crop plant which removes a large amount of nutrient material from the soil is known as a "heavy feeder" and one which removes little as a "light feeder." What factors can you think of which would cause plants to differ in this respect?

172. The salts taken from the soil by one plant are often very different in kind and amount from those taken in by another plant. To what factors may these differences be due?

173. One crop often needs a different fertilizer from another. To what physiological differences in the two crop-plants may this be due?

174. How do submersed water-plants get their salts?

175. Some fertilizers, when applied very abundantly, will often kill plants. Why?

176. A spray-solution which is strongly concentrated will often kill plants to which it is applied. Why?

177. A spray-solution which will kill one plant may not kill another. Explain.

178. Strong spray will often kill the young and growing parts of a plant but not the older portions. Why?

179. If a very strong spray (such as lime-sulphur, used against certain bark-insects of fruit trees) is to be applied to a tree, why must this be done only when the tree is leafless?

180. In such places as gravel walks and tennis courts it is often customary to kill weeds by sprinkling salt upon them. Why is this practice effective? Why is it not widely used in killing farm weeds?

181. *How is it possible for some plants to live on salt-marshes and sea-beaches while others cannot?*

182. Desert plants and salt-marsh or sea-beach plants frequently show similar modifications in structure. Explain.

183. *Why do salt-marsh or sea-beach plants usually die if subjected to fresh water?*

184. The sap concentration in the cells of parasitic plants has been found to be higher than in the cells of the plants upon which they are parasitic. Explain.

185. Why do dried currants, raisins, and prunes swell so much when placed in water?

186. When berries are cooked with little sugar they are apt to burst. When cooked with much sugar they are apt to collapse. Explain.

187. Vegetables usually cook more quickly if they are not salted while cooking. Explain.

188. Celery, sliced cucumbers and similar vegetables are often placed in water for a while before they are served. What effect does this produce and why?

189. Why are we thirsty after eating much salt or sugar?

Note.—In the five following questions, remember that decay is due to the activity of bacteria, which are merely very small plant cells (p. 285).

190. Why is salt such a good perservative of vegetables, meat, fish, and other foods?

191. Which will "keep" better if exposed freely to the air, grape juice or grape jelly? Why?

192. Old-fashioned preserving of fruit was done by the "pound for pound" method, a pound of sugar being used for every pound of fruit. Why was this method successful even in the absence of boiling or any other means of sterilization?

193. What is the fundamental difference between preserving food by salt and preserving it by benzoate of soda or a similar substance?

194. A little salt placed in the water in which cut flowers are standing will often cause them to keep fresh longer than they otherwise would. Explain. Would a large amount of salt in the water have the same result? Explain.

195. *What causes the root-hairs to force themselves in among the* soil particles?

196. Growing roots and stems often exert tremendous pressures, sometimes sufficient to split and lift heavy rocks. What causes this expansive power?

197. Rocks are sometimes split apart, in quarrying, by the insertion of dry wooden wedges into drills or cracks. These wedges are then wetted, and their swelling exerts a powerful pressure. How different in its origin is this pressure from that exerted by a tree-root which splits open a rock?

198. Rapidly growing beets, turnips, and similar fleshy plant parts sometimes crack open during growth. Why?

199. Water is sometimes forced from the leaves of a plant in the form of droplets. Why is this and under what conditions is it likely to take place?

REFERENCE PROBLEMS

22. Are the "root-crops" (such as carrots, parsnips, turnips, and beets) usually annual, biennial or perennial plants? Why?

23. Are there any fleshy-rooted plants which do not have tap-roots?

24. What important crop-plant is propagated by buds formed on its roots?

25. When and by whom was the Cell Theory first formulated?

26. When and by whom was the term "protoplasm" in its present sense first used?

27. Who discovered that every cell has a nucleus?

28. What do we mean by saying that protoplasm is a *colloidal* substance?

29. State two fundamental differences between the typical plant cell and the typical animal cell. With what general differences between animals and plants are these cell differences connected?

30. What prevents the cells of a plant from falling apart?

31. Botanists distinguish between *physical* drought and *physiological* drought. In what does this difference consist?

32. What is the chemical composition of the ash of three important crop-plants? (Take figures from any reliable determination.) How does it happen that the substances and their proportions are different in the different crops?

33. What is the difference between a *nutritive* and a *balanced* solution for plant growth?

34. What relation is there between the *osmotic* pressure of a substance and the *gas* pressure exerted by this substance in its gaseous state?

35. Give the derivation of the following terms and explain in what way each is appropriate:

Protoplasm	Vacuole	Osmosis
Cytoplasm	Plastid	Imbibition
Nucleus	Diffusion	Plasmolysis

CHAPTER V

THE LEAF AND ITS FUNCTIONS

The vegetative organs of the plant naturally fall into two groups: The root-system, situated in the soil and concerned primarily with the absorption therefrom of water and certain nutrient materials; and the stem and leaves (together called the *shoot*), which unfold in the air and are concerned primarily with the manufacture of food, the raw materials for which they

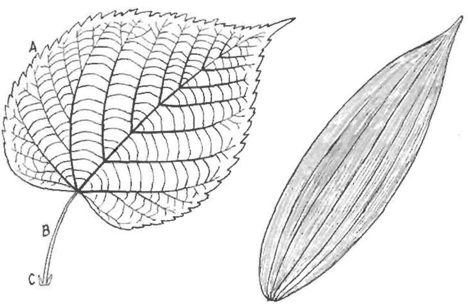


Fig 31.—Two types of leaf-venation. At left, netted-veined leaf of Linden. *A*, blade. *B*, petiole. *C*, stipules. At right, parallel-veined leaf of Solomon's Seal.

derive from both air and soil. Of the two members of the shoot-system the leaf is the primary and more important one, the stem serving merely to expose the leaves to light and air and to provide a means of communication between them and the root-system. It is logical, therefore, for us to follow our study of the root with a study of the leaf.

The Structure of the Leaf.—Before we can understand clearly the functions which the leaf performs, we shall need to observe with some care its rather complicated structure.

External Structure (Figs. 31 and 32).—Externally, the typical leaf consists of a broad, flat, and thin portion, the *blade*, which is the seat of its important activities. This is green in color and provided with a system of ribs or *veins* of stouter texture than the rest of the tissue. The blade may sometimes be attached directly to the stem, but is usually supported by a leaf-stalk or *petiole*, which holds it out in a place favorable for the performance of

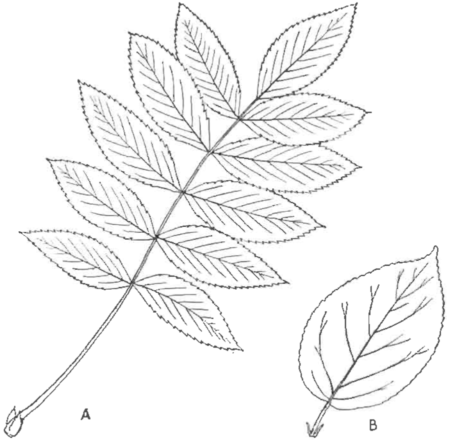


FIG. 32.—Simple and compound leaves. *A*, compound leaf of Mountain Ash, with eleven leaflets. *B*, simple leaf of Apple.

its functions and serves as a highway for transportation of water and food between blade and stem. At the base of the petiole are often two small appendages, the *stipules*, the function of which is in many cases obscure.

Leaves vary widely in size, shape, texture, margin, venation, and other characters. In its outline the blade may be even, or it may be lobed or sometimes actually divided into separate portions, the *leaflets*, in which state the leaf is said to be *compound* (Fig. 32). The margin is sometimes quite smooth, but

is more commonly broken into teeth of various sizes. The vein-system (Fig. 31), is either *parallel* where the veins run side by side with no conspicuous branches; or *netted*, where they divide and anastomose repeatedly. The petiole and stipules vary greatly in their development.

Internal Structure (Fig. 33).—Internally, the structure of the leaf is highly differentiated. A transverse section cut at right angles to the surface of the blade (Fig. 34) displays three important tissues: The *epidermis*, or protective covering; the *mesophyll*,

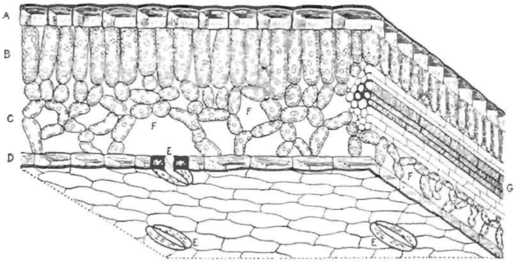


FIG. 33.—A small piece of a typical leaf-blade, seen in three planes and highly magnified. A, upper epidermis, covered by the cuticle (in black). B, palisade layer. C, spongy layer. D, lower epidermis, covered by cuticle. E, stoma (in one case seen in section). F, air space. G, vein, cut lengthwise.

constituting the major portion of the leaf substance, and the *veins*, each of which is a separate fibro-vascular bundle and represents a final branch of the vascular system which runs through root and stem.

The epidermis covers the entire leaf surface and is usually but one cell-layer in thickness. Its cells are generally thin-walled and are filled with a transparent cell-sap. Spread over the outside wall is a thin, waxy, water-proofing layer, the *cuticle*, extending from cell to cell and forming a continuous skin which covers the epidermis. It is usually much thicker on the upper than on the lower surface of the leaf. The epidermis is not an unbroken layer but is provided with minute openings, the *stomata* (singular, *stoma*), through which an exchange of gases between the tissues of the leaf and the outside air may take

place (Fig. 35). These are much more numerous in the lower epidermis than in the upper, and, indeed, are often absent from the latter altogether. Each stoma is a slit-like pore formed by

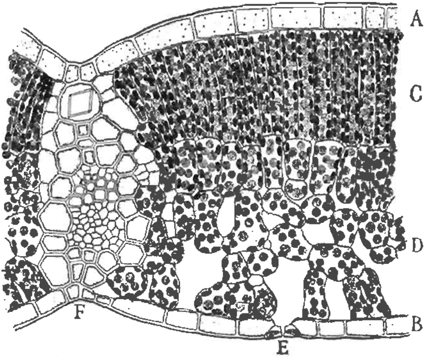


FIG. 34.—Cross section through the blade of a typical leaf. A, upper epidermis, covered with cuticle. B, lower epidermis, also covered with cuticle. C, palisade layer of the mesophyll. D, spongy layer of the mesophyll. E, stoma. F, vein. (*After Kny. From Ganong, "Textbook of Botany", copyrighted by the Macmillan Company. Reprinted by permission*).

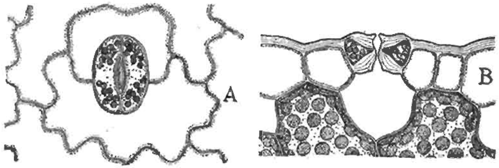


FIG. 35.—A stoma. A, face view, showing the two guard cells (containing chloroplasts); the pore between them, and several adjacent cells of the epidermis. B, transverse section, with the two guard cells, several adjacent cells of the epidermis, and a portion of two palisade cells below. (*After Kny. From Ganong, "Textbook of Botany", copyrighted by the Macmillan Company. Reprinted by permission*).

the pulling apart of two modified epidermal cells, the *guard-cells*, which are unlike other cells of the epidermis in containing chlorophyll. These guard-cells are so constructed that when

plump and turgid with water they tend to pull apart, thus enlarging the opening. On becoming limp and partially collapsed, however, they spring together again and close it. The degree of stomatal opening is thus continually fluctuating as the water supply of the guard-cells rises and falls in response to changing internal or external conditions.

The mesophyll consists of tissue which is characteristically thin-walled, soft, and green. The cytoplasm within its cells contains very small, roundish bodies, denser than the rest of the living substance, and green in color. These are the *chloroplasts* which contain within them the green pigment *chlorophyll*, to which the characteristic color of foliage is due. The mesophyll is not a homogeneous tissue but in typical leaves is divided into two main regions. That part lying next to the upper side of the leaf is composed of cells which are elongated at right angles to the leaf surface, packed rather closely together, and provided with a great abundance of chloroplasts (Fig. 36). This region is known as the *palisade layer* and here is carried on most actively the process of food-manufacture or photosynthesis. The lower region of the mesophyll consists of a mass of cells which are so very irregular in shape that large air-spaces occur between them, and a very loose, sponge-like tissue, the *spongy layer,* is produced. These air-spaces communicate directly with the outside air through the stomata. Chloroplasts are present in the spongy layer, but not abundantly. Through the exposure to the air of a large area of cell-surface, opportunity is provided in this portion of the mesophyll for those gas-exchanges which are continually taking place between the leaf and the atmosphere, such as the absorption and excretion of both carbon dioxide and oxygen, in the processes of photosynthesis and respiration, and the evaporation of water in the process of transpiration.

Running through the blade are the fibro-vascular bundles or veins, the channels by which the leaf tissues are kept in communication with the rest of the plant. The main veins are stout, often projecting somewhat below the lower surface of the blade. These break up into smaller and smaller veins, and finally into minute veinlets which consist of only a few cells. Each vein is surrounded by a *bundle-sheath* of heavy-walled cells, to which most of its rigidity is due. Within this are two tissues: The wood, consisting largely (as elsewhere in the plant body) of elon-

gated, water-conducting cells, the *tracheids* and *ducts*, which distribute the water and dissolved substances brought up through the stem from the root; and the bast, consisting of especially modified cells, the *sieve-tubes*, which collect from the mesophyll

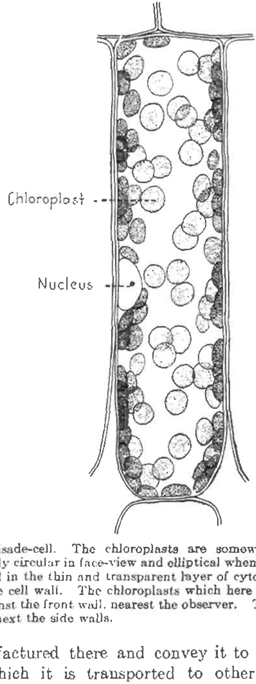


FIG. 36.—A palisade-cell. The chloroplasts are somewhat biscuit-shaped bodies, being roughly circular in face-view and elliptical when seen from the side. They are embedded in the thin and transparent layer of cytoplasm, their broad faces parallel to the cell wall. The chloroplasts which here appear circular are therefore lying against the front wall, nearest the observer. Those which appear elliptical are lying next the side walls.

the food manufactured there and convey it to the bast of the stem, along which it is transported to other parts of the plant.

The petiole, usually circular in cross section, has within it a cylinder or half-cylinder of fibro-vascular bundles which are con-

tinuous with the main veins of the blade above and which enter directly into the vascular cylinder of the stem below.

Photosynthesis.—The primary activity of green leaves is the *manufacture of food* from certain simple inorganic materials—carbon dioxide and water—by energy derived from light. This process of *photosynthesis* is fundamental in organic nature, for it is not only an essential function of green plants themselves but is of the utmost significance to animals and man, because it constitutes the sole ultimate source of food in the world. Food is primarily a storehouse of *energy* and of *body-building materials* for living things. In the green parts of plants, and nowhere else among organisms, is active or *kinetic* energy—in this case the energy of light—converted into a latent or *potential* form, readily available to living organisms for use in maintaining their vital activities; and, moreover, in green plants alone are produced those fundamental organic materials out of which plant and animal bodies are constructed. All the complex metabolic changes which later take place in the organic world are simply elaborations or simplifications of the primary products of photosynthesis. A more detailed account of the various types of foods and their uses, and of the energy-relations of the plant, will be given in our chapter on Metabolism.

Materials.—The materials combined by the plant in this process are but two—water and carbon dioxide. Water is absorbed from the soil by the roots, passes upward through the stem, the petiole, and the veins of the leaf, and thence enters the mesophyll cells. None is obtained by the leaf directly from the atmosphere. It should be remembered that only a relatively small portion of the water taken in by the plant is used in food-manufacture; for much the larger part soon leaves the plant again, passing out of the leaf into the air by transpiration. The carbon dioxide used in photosynthesis is derived entirely from the air. Here it is always present, but in such small quantities that it constitutes only about three parts in ten thousand of the atmosphere or three hundredths of 1 per cent. Experiments have shown that a higher concentration would be advantageous to plant growth, since up to a certain point the rate of photosynthesis rises if the proportion of carbon dioxide in the air is artificially increased. It is through this comparatively rare gas alone that the plant derives its supply of carbon, that element so vitally necessary to all living organisms. No other carbon compounds, not even the abundant

supplies present in the complex organic materials of humus, can apparently be drawn upon by ordinary green plants. Carbon, oxygen and hydrogen, together with the seven essential elements derived from the soil, constitute the necessary chemical basis for plant life.

Mechanism.—The mechanism or apparatus by which water and carbon dioxide are combined is the remarkable green pigment *chlorophyll.* This is present only in the *chloroplasts*, portions of the cytoplasm slightly denser than the rest. Chloroplasts may be few and large in certain lower plants but in the higher ones are almost always small, numerous, and more or less spherical in shape. They are most abundant in the palisade layer of the leaf. As to chlorophyll itself we know comparatively little except that it is a complex protein and contains magnesium. Iron is essential for its production but apparently does not enter into the construction of the substance itself. The presence of light is also necessary for the full development of chlorophyll, as is shown by the pale color of leaves which have grown in darkness. We are even more ignorant as to the manner in which chlorophyll operates in bringing about the union of carbon dioxide and water, nor have we yet succeeded in imitating this process in the laboratory. We know, however, that chlorophyll does not contribute material to the product formed and that it is not used up itself in the process, and we may therefore infer that it acts somewhat as does a catalyzer.

Associated with chlorophyll is usually another pigment or group of pigments, yellow in color instead of green, to which the general terms *xanthophyll* or *carotin* are given. These are not concerned with photosynthesis and their function is poorly understood. To them are due most of the yellow colors which occur in plants. Chlorophyll is a very unstable compound and tends to break down quickly when extracted from the leaf or when the leaf loses its vitality, but the yellow pigments are much more resistant and often survive long after chlorophyll has disintegrated.

Energy.—Energy is necessarily expended in the process of breaking up the molecules of water and carbon dioxide and recombining their atoms into a new compound. We know that this energy is derived not from heat, as in so many cases, but entirely from *light*, which thus plays an essential part in the physiology of plants. According to the most widely accepted theory, light

is due to minute and enormously rapid vibrations, the length of the vibration—its *wave-length*—determining the color of the light produced. Sunlight, or any white light, is composed of vibrations of a great variety of different wave-lengths, but when such light is passed through a prism these become sorted out into a many-colored *spectrum*. The visible spectrum runs from the red rays, the wave-length of which is approximately 750 millionths of a millimeter, to the violet ones, where it is approximately 400. These visible radiations are by no means the only ones which occur, however. Rays of longer wave-length than red—

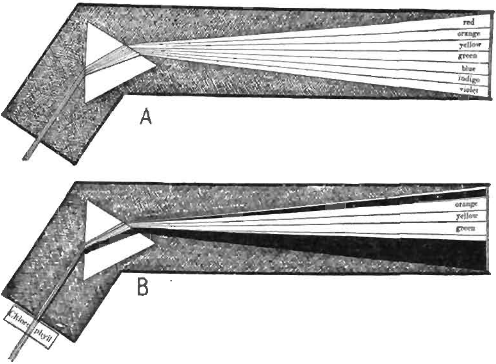


FIG. 37.—Diagrams of a spectroscope, showing light broken up by a prism into its constituent portions, which form a spectrum. *A*, spectrum of white light. *B*, spectrum of light which has passed through a chlorophyll solution, showing the dark absorption bands in the red and the blue. (*From Ganong, "The Living Plant", Henry Holt and Co.*)

the infra-red rays—pass gradually into heat-waves, and those shorter than violet—the ultra-violet rays—are active chemically. When falling upon different objects, light behaves differently. All of it may be absorbed by the object and converted into heat or some other form of energy, the object then appearing black; or all may be reflected, the object then appearing white; or certain wave-lengths may be absorbed and certain others reflected, the object in such a case displaying to our eyes the color of

the light which it reflects. We know, for example, that a green substance like chlorophyll absorbs in general those wave-lengths which are not green and reflects those which are green or greenish-yellow. We can determine more accurately, however, the kind of light which is absorbed by a substance, if we break up into a spectrum the light which has passed through that substance. Such a spectrum displays perfectly dark regions, or *absorption bands*, in those portions which correspond to the particular kinds or wave-lengths of light which the substance has absorbed. The absorption spectrum of chlorophyll (Fig. 37) shows a narrow, sharp, black band in the orange-red and a wider, less definite one in the blue, thus indicating that it is chiefly these two kinds of light which chlorophyll absorbs, and suggesting that the red and blue rays in sunlight, and no others, furnish the energy used in the process of photosynthesis. Chlorophyll possesses the remarkable power of utilizing energy from this source in the manufacture of food, an ability that is unique in the organic world.

The intensity as well as the character of the light affects the rate at which photosynthesis proceeds. The process begins at illuminations of very low intensity, reaches its maximum at about that of bright diffuse daylight, and decreases again in light which is so bright as to injure protoplasm. Photosynthesis may be readily accomplished in artificial light of the proper intensity and wave-lengths.

Given a supply of the necessary raw materials, a sufficient temperature, the presence of chlorophyll, and light of proper character and intensity, photosynthesis may go on anywhere in the plant. Although these conditions are preëminently fulfilled in the mesophyll of the leaves, they may also be present to a lesser extent in petioles, stipules, calyx-lobes, and other organs, thus insuring a utilization of these regions to produce a small supplementary food supply.

Products.—Let us now turn from a consideration of the necessary conditions for photosynthesis to a study of its products. The details of the process whereby carbon dioxide unites with water are not yet known, but the formation of formaldehyde (CH_2O) is perhaps one of the preliminary steps. The first product which can be recognized, however, and a substance which is therefore of unique interest, is *glucose* or *grape sugar*, $C_6H_{12}O_6$, formed according to the following equation:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

Glucose is present in the sap of practically all plant cells. It is the fundamental carbohydrate and the basis for all other foods; and from it are ultimately derived, through the action of enzymes and by various additions and chemical modifications, all the organic compounds of plants and animals.

The presence of a large amount of sugar in a chlorophyll-bearing cell results in a stoppage of its manufacture there, and is disadvantageous for other reasons. We find, accordingly, that before photosynthesis has long continued, the resulting sugar becomes converted into another type of carbohydrate, *starch* $(C_6H_{10}O_5)_n$.* Starch is complex and insoluble, occurring in minute but definite bodies or *grains*, the size, shape and markings of which are characteristic and constant in any plant species. The starch molecule is very large—just how large we do not know—and is derived through the combination of many glucose molecules, with the liberation of a molecule of water from each, thus:

$$nC_6H_{12}O_6 - nH_2O = (C_6H_{10}O_5)_n.$$

Neither sugar nor starch are accumulated in very great quantities in the leaf-blade, for most of the products of photosynthesis are removed shortly after their production to those regions of the plant where they are to be used or stored.

By-product.—In the recombination of the atoms of carbon dioxide and water out of which glucose is produced there is evidently a surplus of oxygen, and we find this oxygen given off as a by-product of photosynthesis, passing forth into the air continually from green plants during daylight. This is of little significance to the plant itself but is often important to other organisms.

Photosynthesis is, therefore, a constructive process by which the food of the plant is manufactured from very simple inorganic materials, through the agency of the characteristic substance chlorophyll, and by energy derived from light. The significance of photosynthesis lies in the fact that it is the only process among living things whereby organic compounds are built up from simple inorganic substances, with the resultant storage of energy. All other chemical changes in plants and animals are concerned either with the transformation of one type of organic material

* n stands for the unknown number of smaller molecules which are united into one of the large and complex ones of such a substance as starch.

into another or with the breaking down of complex organic compounds into simpler ones. Photosynthesis alone is fundamentally constructive, and the activity of green plants thus underlies that of all other organisms.

Transpiration.—The lower portion of the mesophyll, or the spongy layer, is not concerned primarily with photosynthesis but with the interchange of gases between plant and atmosphere. Notable among these interchanges is the evaporation of water from the tissues and its passage into the air, a process which we know as *transpiration*.

The Importance of Water.—The water-relations of a plant are of the utmost importance to it and profoundly influence its structure and activities. We have seen that water constitutes the major portion (75 to 90 per cent) of plant tissues in general, and a very much larger share of protoplasm itself. An abundance of water keeps the cells plump, and by maintaining the turgidity of the tissues, enables the soft parts of the plant to preserve their firmness and to function successfully. Water is one of the raw materials entering into the process of photosynthesis. It is the solvent of the mineral nutrients, which can enter the plant and move about within it only when in solution, and in watery solutions all the important physiological processes of the plant take place. The maintenance of an abundant supply of water in its tissues is therefore essential for the life and growth of the plant.

To this end the primary requisites are evidently the presence of a sufficient amount of available water in the soil and its abundant absorption therefrom by the roots. Of no less significance in the water-relations of the plant is the process by which this water evaporates from the plant tissues and passes into the air. Absorption must equal or exceed transpiration if the plant is to thrive, for should there be a deficiency in income or an excess of outgo, a shortage of water will result in the tissues, and the plant will suffer accordingly.

Only a very small fraction of the water which enters the root-hairs and passes upward to the leaves takes part in the manufacture of sugar. The remainder becomes distributed through the cells of the spongy layer and evaporates from their moistened walls, departing through the stomata as water vapor (Fig. 38). A smaller amount may be evaporated directly from the surface of the epidermal cells. During the growing season a constant

stream of water is thus passing through the plant body, entering at the root-hairs and leaving through the stomata. The total quantity of this water often amounts to several hundred times as much as the final dry weight of the plant itself (Fig. 39).

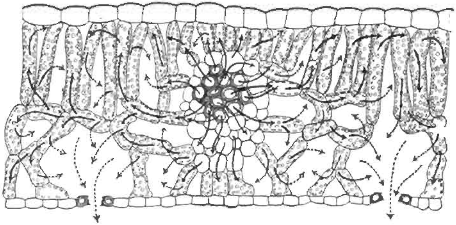


FIG. 38.—Transpiration from the leaf-blade. Cross-section of a blade including a vein. Arrows indicate passage of water from the vein, through the mesophyll cells, into the air-spaces, and out through the stomata. Solid arrows, liquid water; dotted arrows, water-vapor.

The Rate of Transpiration.—The rate of water-loss varies greatly according to the kind of plant, the soil conditions, the season of the year, the time of day, and various environmental factors. As a general rule, we find that the rate tends to increase under conditions which favor increased evaporation, such as high temperature, bright light, rapid air movement and low humidity; and to decrease under environments of the opposite character.

Transpiration is by no means controlled entirely by factors which influence evaporation alone. The rate of water-loss from a given leaf-surface and from an equal area of free water do not rise and fall exactly together, the transpiration from the living leaf sometimes being relatively higher and sometimes relatively lower. There must, therefore, be factors in the leaf itself (as opposed to those in the external environment) which tend to accelerate or to retard transpiration. The most important of these is doubtless the opening and closing of the stomata, which we have already discussed. Changes in the concentration of the sap in the mesophyll cells also probably determine to some extent the rate at which water evaporates from their surfaces.

The actual amount of water transpired during the growing season may be large or small, depending on the size of the plant,

its leaf-area, its transpiration-rate, and the moisture and fertility of the soil. Of most significance to the plant, however, is not the actual bulk of transpiration, but the efficiency with which the water is used. This is determined by comparing the weight of

FIG. 39.—The water-requirement of a corn plant. The amount of water transpired from this corn plant, during its growth and development, would under normal conditions fill the barrel.

the total water transpired with the weight of the dry plant material ultimately produced, their quotient being known as the *water-requirement* of the plant. Thus when we say that the water-requirement of corn under certain conditions is 400, we mean that for every gram of dry weight of corn plant produced

at maturity, there have been transpired through its leaves 400 grams of water. Species vary markedly in their water-requirement, and so do plants of the same species when grown under different conditions.

The Significance of Transpiration.—Excessive water-loss is an ever-present danger to land plants, and many structural modifications have been developed by various species, or may appear in particular individuals growing under dry conditions, which tend to reduce this loss. The question therefore arises as to whether transpiration is an unmixed evil, made necessary by the fact that the stomata must be open to allow the exchange of gases which take place in photosynthesis; or whether it is really a function of the leaf and performs a useful part in the plant's economy. It was long thought that water must be taken in through the roots in large quantities to insure an abundant absorption of nutrient materials from the soil, but a fuller understanding of the phenomena of osmosis and root absorption shows the fallacy of this conclusion. It has also been contended that transpiration is useful in concentrating the very dilute solutions of nutrient salts taken from the soil—"boiling them down," so to speak. We have seen, however, that the factors which determine the entrance of nutrient materials into the plant preclude such an explanation; and, indeed, experiment shows that the amount of salts absorbed is practically independent of the amount of water transpired. Transpiration from the leaves, however, is evidently what causes the *transpiration stream*, or continuous movement of water from root to leaf through the lifeless ducts in the wood of the stem. We shall consider this movement more fully when discussing the functions of the stem; but it is well to note here that by this stream the dissolved substances are transported bodily from the central cylinder of the root upward throughout the plant as far as the ramifications of the dead conducting elements of the wood extend. This movement is probably far more rapid than would result through diffusion from cell to cell, and in tall plants, particularly, the transpiration stream probably performs a distinct service in distributing rapidly throughout the plant the supply of nutrient materials absorbed from the soil.

Transpiration is also of distinct usefulness in regulating the temperature of the leaf. The blade absorbs much more energy than it uses in photosynthesis, particularly in bright light; and

the excess, as heat, would sometimes raise the temperature of the tissues dangerously, were it not absorbed in evaporating water from the mesophyll cells.

Transpiration is carried on primarily in the leaves, but may occur in any other organs which are exposed to the air. Excessive loss of water is often prevented in such regions by the development of cell layers with corky walls.

QUESTIONS FOR THOUGHT AND DISCUSSION

200. Are leaves generally more variable in their area or in their thickness? Explain.

201. What general difference in shape is there between netted-veined and parallel-veined leaves?

202. Leaves on the same plant often differ markedly in the length of their petioles. How do you explain these differences?

203. Name three functions which the veins of a leaf perform.

204. In leaves where the veins are much stouter than the thickness of the blade, they usually stand out on the *under* side of the leaf and thus leave the upper surface smooth. What are the advantages of this arrangement to the plant?

205. Of what advantage, and of what disadvantage, is it to plants of temperate climates to shed their leaves in the winter?

206. The leaves of "evergreen" trees do not remain permanently on the tree but each year's crop lives only a few seasons and then drops off. Why should these leaves not continue to live and function indefinitely?

207. The upper epidermis and its cuticle are almost always thicker than the lower. Explain.

208. The cells of the leaf-epidermis usually have transparent walls and a colorless cell-sap. Of what advantage is this to the plant?

209. Some parasitic fungi attack only the epidermis of the leaf, but they often cause the death of the leaf and even of the entire plant. Explain.

210. How do you explain the fact that the palisade layer is next the upper surface of the leaf and the spongy layer next the lower?

211. What does the plant gain by having the cells of the palisade layer elongated at right angles to the leaf surface?

212. The upper surface of each epidermal cell of the leaf is often slightly convex. How may this perhaps be of advantage to the plant?

213. Do you think that photosynthesis is carried on in the spongy layer at all? What evidence have you for your belief?

214. Name at least two advantages which the plant derives from having its stomata more abundant on the lower surface of the leaf than on the upper.

215. Stomata are usually absent in the leaves of submersed water-plants. Explain.

216. Why does washing the leaves of house plants often improve the health of the plants?

217. In cities where soft coal is burned and there is much coal-dust in the air, all trees suffer, and evergreen trees in particular find it very difficult to live. Explain these facts.

218. In what ways is the supply of carbon dioxide in the atmosphere being replenished?

219. Do you think that the continual removal of carbon dioxide from the atmosphere by green plants in photosynthesis will reduce the amount of this gas which is present there? Explain.

220. The great deposits of coal formed in the Coal Period, millions of years ago, have sometimes been pointed to as evidence that carbon dioxide was much more abundant in the atmosphere then than now. What basis is there for such a conclusion?

221. As the carbon dioxide in the leaf is removed by photosynthesis, what causes a fresh supply to enter the stomata from the outside air?

222. What factors determine the rate at which carbon dioxide enters the leaf?

223. In some greenhouses the plants are "fertilized" by pouring carbon dioxide from a chimney into the air around the plants. Why does this increase plant growth and why would it be impracticable out-of-doors?

224. The fact that carbon dioxide is more soluble in cold water than in warm has been cited as one of the reasons why seals, walruses, polar bears, and even Eskimos are able to thrive in such large numbers so far north. Explain.

225. A solution of chlorophyll outside the plant, when exposed to sunlight and in the presence of carbon dioxide, will not produce sugar. How do you explain this?

226. Which is darker green in color, the upper or the lower surface of the leaf? Why?

227. Why is the intensity of green color in its foliage good evidence as to the health of a plant?

228. The stems and leaves of parasitic plants, such as mistletoe and dodder, are either very pale green or are some other color than green. Explain.

229. Why do autumn leaves and dying leaves often turn yellow?

230. When cows are turned into fresh pasture in the spring, their butter turns deep yellow. Why? Why does it not turn green?

231. In order to "bleach" celery plants, gardeners cover them with earth or wrap them in paper. Why is this practice effective in securing the desired result?

232. What is the orientation (vertical, horizontal, oblique or other) of an ordinary leaf blade? Explain.

233. The lower leaves on a plant or branch often hang downward somewhat obliquely, in contrast to the upper leaves, which are generally horizontal. Of what advantage is this fact to the plant?

234. In many herbaceous plants the lower leaves have long petioles but higher up on the stem the petioles gradually decrease in length and often are quite absent in the upper leaves. Explain.

235. Of what advantage and of what disadvantage is it to a plant to have its leaves very deeply cut or lobed?

236. Are opposite leaves usually broader or narrower than spirally arranged ones? Explain.

237. Why are plants with upright, grass-like leaves usually more successful in open, sunny situations than are plants with broad, horizontal leaves?

238. Why is it easier to maintain a lawn under elms or apple trees than under maples?

239. In just what part of a tree are most of its leaves borne? Why?

240. Why are the lower limbs of a tree growing in the forest usually dead?

241. Many plants are able to thrive in relatively deep shade on the floor of the forest, where the lower limbs of the forest trees have long since died. How can this be?

242. Seedlings of most forest trees will grow and thrive on the forest floor in rather deep shade, but the lower limbs of mature trees of the same species, if subjected to similar light conditions, will soon die. Of what advantage to the plant is this difference between young and old individuals?

243. Most of our woodland "wild flowers" (herbaceous plants which grow on the forest floor), thrive and blossom in early spring. Why?

244. Where does the light come from which is utilized by the chlorophyll of the spongy layer?

245. Leaves exposed to bright sunlight are thicker than those growing in the shade, even on the same plant. Explain.

246. How would you determine what wave-lengths of light are of most importance in photosynthesis?

247. Would you predict that a plant would thrive better in red light or in green light? Why?

248. Plants grown in winter in greenhouses rarely grow as rapidly as do plants out-of-doors in the summer, even though the temperature is kept as high. Explain.

249. Other things being equal, why do most plants grow faster in June than later in the summer?

250. *Crops are necessarily planted much later near the northern limit* of their range than farther south, but in many cases their growth-rate is so much more rapid that they reach maturity almost as soon. Explain.

251. In the North Sea fisheries, it has been found that the size of the season's catch of fish tends to be greater in seasons when there has been much sunshine than in seasons which have been relatively cloudy. Explain.

252. Some plants (such as the fungi) are able to thrive in the absence of light. What other important physiological differences must there be between these and ordinary green plants?

253. Of what advantage is it to the plant to have the sugar which is produced by photosynthesis converted rapidly into starch?

254. It is sometimes said that forests tend to "purify the air." What basis in fact is there for this statement?

255. Why do animals in an aquarium thrive better if green water-plants are growing in the aquarium?

256. Compare in detail the leaf of a green plant with a manufacturing establishment.

257. From the point of view of living things, which do you think are the three most important chemical elements? Why?

258. Which do you think would be worse for a tree, the loss of half of its branches by an ice-storm or of all of its leaves through an insect attack? Explain.

Note.—By the term *dry weight* is meant the weight of all the material in a given body except its water. It is usually determined in the laboratory by drying the material in an oven at about 100° C.

259. Would the dry weight of a leaf be greater in the morning or in the following evening? Why?

260. Will seedlings grown in the dark increase in actual weight? in dry weight? Explain.

261. The leaves of parasitic plants are often very small. Explain.

262. How do submersed water plants carry on photosynthesis?

263. Give at least three reasons why trees often fail to thrive in a city.

264. From your knowledge of plants, do you think that they need a rest at night, or would they thrive continuously if the light were continuous?

265. Some crops produce a much larger amount of dry weight per acre than others. Explain how this can be.

266. The potato beetle does not attack the potato tuber, but eats only the foliage of the potato plant. Why does it harm the crop?

267. Why does repeatedly cutting off their tops finally kill persistent perennial weeds?

268. If a man wants to clean out suckers and low shrubs from pasture-land, should he mow them down in summer or in winter? Why?

269. Is there any basis in fact for the belief held by some farmers that there is one particular day in summer when suckers and brush should be cut down, if you want to kill them off?

270. Which will give better and larger flowers the next season, tulip bulbs which are pulled up immediately after flowering or those left in the ground until after the leaves have withered? Why?

271. Why should a new field of asparagus not be harvested until two or three years after the young plants have been set out?

272. Which should you keep mown more closely, a newly seeded lawn or an old one? Why?

273. Should lawn grass, when cut, be raked off the lawn or not? *Explain.*

274. Other things being equal, is it better to plant the rows of a garden east and west, or north and south? Why?

275. State two reasons why a garden planted near a shade tree is apt to be unsatisfactory.

276. Do you think that transpiration is essential for the life of the plant? Explain.

277. What process in animals may be said to correspond roughly to the transpiration of plants? In what respects are the two processes similar?

278. From your knowledge of osmosis, explain why it is that "the amount of salts absorbed is practically independent of the amount of water transpired by the plant".

279. Just where in the leaf does evaporation take place during the process of transpiration?

280. What makes water leave the cytoplasm of the spongy layer cells (or any others) and wet the cell walls?

281. Why is it that the air in the air spaces of the spongy layer of the leaf does not become so saturated with moisture that evaporation, and consequently transpiration, will no longer take place?

282. In general, the faster a plant loses water by transpiration, the faster it will absorb it from the soil. Explain.

283. Do you think that a plant would be able to thrive and grow permanently in an atmosphere which is completely saturated with moisture? Explain.

284. Will transpiration be more rapid or less rapid if the sap of the mesophyll cells increases in concentration?

285. Why does transpiration take place so much faster in wind than in still air?

286. Why do florists usually water the walls and walks of a greenhouse as well as the plants themselves?

287. Why does a plant wilt if its water supply fails?

288. Some plants wilt much more readily than others. What factors may be responsible for these differences?

289. Why is a wilted plant unable to carry on its functions as well as one that is in a normal, turgid condition?

290. Why will a plant sometimes wilt even though the soil in which it is growing is abundantly supplied with water?

291. Why does a plant which has wilted in the daytime usually revive at night, even though no rain falls?

292. If a tree is subjected to a severe drought, its leaves wilt but its twigs remain rigid. Explain.

293. In using foliage for wreaths or other decorations, would you choose young leaves or mature leaves? Why?

294. The stomata often tend to close in the middle of a hot day. Explain why this is so and how it is of advantage to the plant.

295. Do stomata tend to open or close if the leaf is exposed to the light? Explain.

296. How will stomata tend to act during the course of a normal period of twenty-four hours during the summer?

297. What is the best time of day to pick flowers, if it is desired to keep them fresh for a long time out of water?

298. Why will cut flowers remain fresh longer if they have been placed in water for a few hours directly after being picked?

299. Do you think that the water requirement of a plant will be higher if it is grown on rich soil or if it is grown on poor soil? Why?

300. Do you think that the water requirement of a plant will be higher if it is grown on moist soil or if it is grown on dry soil? Why?

301. Do you think that the amount of cultivation which a plant receives will have any effect on its water requirement? Explain.

302. Assuming that the water requirement of corn under a given set of conditions is 400, and that a bucket holds 10 liters, how many buckets of water have passed by transpiration through a corn plant the dry weight of which is 200 grams?

303. Given the same conditions as in Question 302, assume further that three such corn plants are planted in each hill and that the hills are one meter apart each way. If all the water which passes through these plants by transpiration during the season could be collected, how deep a layer would it make over the surface of the field?

304. Why does a shortage of water stunt a plant?

305. Is transpiration apt to be high or low when growth is most rapid? Explain.

306. Plants generally grow faster at night than in the daytime. Why?

307. How do you reconcile the fact that plants grow faster at night than in the daytime, with the fact that light is necessary for the manufacture of food?

308. Plants generally grow faster in wet weather than in dry. Why?

309. Why do plants often suffer from "scalding" after a brief summer shower in the middle of the day?

310. Can you think of any other reason than the presence of shade which may tend to make a forest cool?

311. The planting of rank-growing species like the sunflower has sometimes been thought to reduce the amount of malaria in malarial districts. What basis in fact is there for this belief?

312. Name one way in which the presence of a forest tends to increase the loss of water from the soil and one way in which it tends to decrease it. Do you think that a soil will lose water faster if it is covered with forest or if it is not? Explain.

313. Why is the effect of a killing frost in the fall usually not evident on the following morning until the sun has been up for some time?

314. If a plant has been "touched" by the frost but not killed, why is it sometimes possible to restore it by sprinkling it with water and placing it in a cool, shaded place?

315. What structural modifications do you know of in plants which tend to result in checking transpiration?

316. What characteristics must drought-resistant plants possess?

317. The leaves of corn and other grasses often roll or curl when it is very hot or dry. Why is this and of what advantage may it be to the plant?

318. The leaves of desert plants are usually leathery, fleshy or very small. Explain.

319. The leaves of *Eucalyptus*, a tree which flourishes in warm, dry regions, hang vertically on the branches. Explain how this is of advantage to the plant.

320. The leaves of "compass plants" are erect and vertical, with their edges pointing approximately north and south. In what two ways may this character be of advantage to the plant?

321. Plants with downy or woolly leaves are very abundant on mountain sides and exposed alpine situations. Why are they particularly suited to such conditions?

322. Why do epiphytes (p. 174) usually have leathery leaves?

323. The leaves of evergreens in temperate regions are usually firm and leathery. Explain.

324. Evergreen trees often suffer from "wind burn" in late winter or early spring, a part or all of their branches dying and turning brown. They do not suffer from this cause earlier or later in the season. Explain.

325. Give two reasons for the fact that plants grown in the shade are usually more tender than plants grown in the bright sunlight

326. Why is the best lettuce grown in early spring?

327. Spring is the best season to transplant a tree. Why?

328. Why is it better to do transplanting on a cloudy or rainy day than on a bright one?

329. Why is it advantageous to cut off the outer leaves of young plants before transplanting?

330. If it is necessary to transplant young trees during the summer, the plants should first be vigorously pruned. Why?

331. Why will potatoes in storage lose weight much faster after sprouts have grown out on them?

332. Why is it best to store apples in a fairly moist place but beans where it is dry?

333. Tobacco growers sometimes cover their plants with cheese-cloth tents. What effect do you think this has on the structure and functions of the tobacco leaves?

REFERENCE PROBLEMS

36. Give an example of a leaf which has assumed some of the functions of a stem.

37. Where is the palisade layer in leaves which stand erect, like those of *Iris?*

38. What various functions may stipules perform?

39. Give the number of stomata found per square centimeter of leaf surface on three species of plants.

40. What is the composition of ordinary air?

41. How many cubic centimeters of air are needed to provide enough carbon dioxide for the manufacture of one gram of starch by photosynthesis?

42. About what proportion of the energy reaching a leaf in sunlight is used in the process of photosynthesis? How does this compare with the amount utilized by a good steam-engine from the burning of coal?

43. About how much sugar is normally manufactured by one square meter of leaf-surface of an average plant during an average summer's day?

44. Are the leaves of "foliage-plants," which are brightly colored (not green) able to carry on photosynthesis? Explain.

45. In the case of some one common crop-plant, give the percentage of dry matter, of water, and of ash which typically compose it. From what source has each been derived?

46. When and by whom was the process of photosynthesis in plants first clearly understood?

47. What is the average annual rainfall in this region? About how much of this is returned to the air by a vigorous crop through transpiration?

48. Give the derivation of the following terms and explain in what way each is appropriate:

Petiole	Stoma	Xanthophyll
Epidermis	Photosynthesis	Chloroplast
Mesophyll	Chlorophyll	Transpiration

CHAPTER VI

THE STEM AND ITS FUNCTIONS

We have shown that the root, which absorbs water and mineral substances from the soil, and the leaf, which carries on the manufacture of food, are the primary vegetative organs of the plant. A third member, the *stem*, connects these two. It forms a conspicuous feature of most plants and in woody species constitutes the great bulk of their bodies. Its functions, though secondary to the major activities which we have mentioned, are nevertheless essential ones. It serves to dispose the leaves in situations favorable for photosynthesis, and provides a highway for transportation between leaf and root. In addition, the stem frequently becomes a storage-organ and may be variously modified for other special functions.

The External Structure of the Stem.—The stem displays a wide range of variation in size and in external and internal structure, according to the habit or growth-form which the plant assumes. In *herbs* (Fig. 40), where the whole shoot dies back to the ground during periods unfavorable to vegetative activity or at the completion of a given cycle, the stem is comparatively slender and soft in texture. In plants with perennial aboveground parts, however, it grows thicker from year to year and becomes hard and woody, forming the stout stems characteristic of *shrubs* (Fig. 41) and *trees* (Fig. 42). In shrubs the stem is comparatively short and slender and is usually much branched, even close to the ground. In trees, it grows taller and is developed for some distance upward into a main stem or *trunk* which may become very thick. Woody stems transitional between these two types often occur.

Buds.—The growth of the stem in length takes place only at certain definite points, where the cells are thin-walled and capable of active division. In many stems, particularly those which are perennial and woody, these growing-points are protected by leaves or scales and are then known as *buds* (Fig. 43). Buds may be *terminal*, developing at the tip of the stem, or *lateral*, arising from

the sides. Within the bud are not only the beginnings of the young stem but of the various structures which are borne upon it, such as leaves and flowers. The *bud scales*, which protect these delicate parts, are usually stout and impervious.

FIG. 40.—An herb. The lark-spur (*Delphinium*).

The terminal bud governs the elongation of the stem, and through the development of lateral buds, *branches* arise. The shape of the aerial portion of the plant is determined primarily by the number and arrangement of these branches and by their rate of growth relative to each other and to the main stem.

In certain herbaceous plants the terminal bud produces a flower or flower-cluster, and the growth of the stem in length usually ceases at this point. Such *determinate* growth is not common among woody plants, however, and their stems continue to elongate indefinitely.

Leaves.—Leaves are borne throughout the length of the stem in herbaceous plants and on the twigs of the current year's

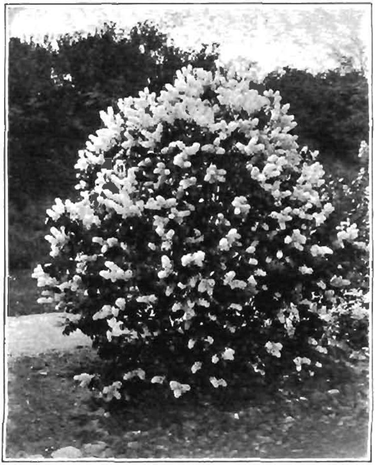


FIG. 41.—A shrub. The lilac (*Syringa vulgaris*).

growth in woody forms (Fig. 44). That point on a stem at which a leaf is attached is called a *node* and the region between two nodes, an *internode* (Fig. 43). The position of the node also governs the position of the lateral bud, for such a bud normally arises only in the leaf *axil*, or upper angle between leaf and stem.

The arrangement of leaves on the stem, or its *phyllotaxy*, may display many different types. If but one leaf occurs at a node the next one above it arises from the other side of the stem, and the arrangement is thus an *alternate* one (Fig. 44). These

two leaves may be exactly half way around the stem from each other, but it is much more common for their angle of divergence to be less than 180° and for the points of attachment of a series of successive leaves thus to form a loose spiral around the stem The closeness of this spiral and the position of the leaves thereon show great diversity, but are generally constant within any par-

FIG. 42.—A tree. The shagbark hickory (*Carya ovata*). (*Courtesy United States Forest Service*).

ticular species. If two leaves arise from the same node they are always directly across the stem from each other and are said to be *opposite in arrangement* (Fig. 43). When there are more than two leaves at a node, they are disposed about the stem in a circle or *whorl*.

Surface.—The surface of a young stem is protected only by an epidermis, but later this is replaced in woody plants by a characteristic layer of corky cells, the *bark*. The necessary exchange of gases between the air and the living tissues of the

stem takes place through the lenticels (Fig. 43), *small spots or* strips where the bark tissue is softer and looser than elsewhere.

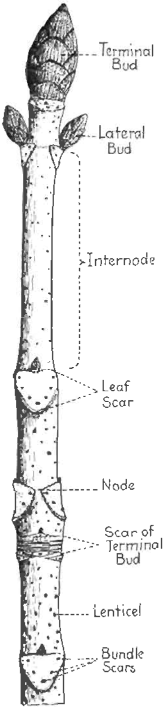


FIG. 43.—A woody twig in winter condition (Horse-chestnut).

Other Stem Types.—The typical upright, foliage-bearing stem has sometimes become radically modified for the performance of

other functions than support and conduction. Many plants have abandoned the erect habit, and their weak, slender stems climb or scramble by various means over other objects or lie prostrate on the ground. In certain herbs the main stem may even become subterranean, in which condition it is known as a

FIG. 44.—Summer (*B*) and winter (*A*) condition of the same woody twig (Cherry) The buds arise in the angle between leaf and steam.

rootstock or *rhizome* (Fig. 45). Typical stems give opportunity for the storage of a certain amount of food reserves, especially in pith and cortex, but in some species this function is so greatly developed that the stem system, or certain parts of it, becomes essentially a storage organ only. This condition exists in most rootstocks, and its extreme development results in a reduction of the stem to a short, thick *tuber* such as we know in the potato (Fig. 46), which is morphologically a stem but now shows little obvious resemblance to that organ. The *bulb* and the *corm* (Fig. 47) are other examples of highly modified underground stems.

The Internal Structure of the Stem.—In the cross section of a typical young stem (Figs. 48, 53 and 54) there may be distinguished the same three types of tissue which are present in the

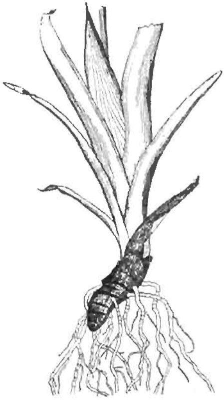


FIG. 45.—Rootstock of *Iris*.

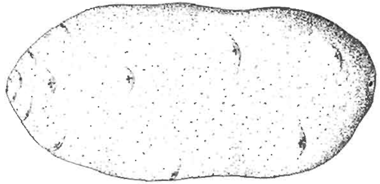


FIG. 46.—Tuber of the potato, showing point of attachment to the parent plant (at extreme right) and numerous buds or "eyes," each in the axil of a reduced and scale-like leaf.

root, but they are arranged somewhat differently. Outside the whole is the *epidermis*, consisting of a single cell-layer, and often replaced entirely, at an early stage, by a zone of *corky bark*.

Beneath this is the *cortex*, varying in thickness but rarely occupying as prominent a place in the stem as it does in the root. Beneath the cortex lies the *fibro-vascular cylinder* which, unlike its counterpart in the root, is arranged in the form of a hollow tube. The core of this tube is occupied by the *pith*, a tissue

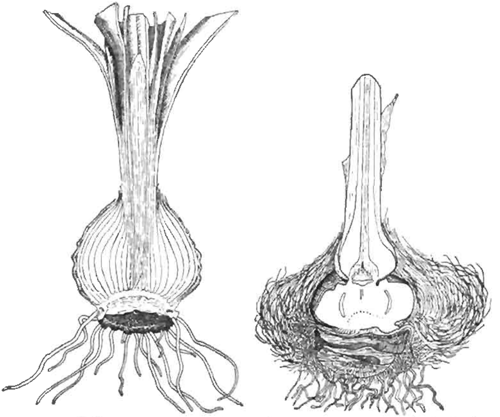


FIG. 47.—Bulb and corm. (*A*), longitudinal section through the bulb of a hyacinth. The short, broad stem bears a cluster of fleshy leaves, the central ones of which grow out as foliage leaves. (*B*), longitudinal section through the corm of a crocus, showing the thick, short stem surrounded by the fibrous remains of old leaf-bases. The remains of corms of three preceding seasons are shown below the present one. The tops of the leaves have been cut off in both illustrations.

much resembling the cortex. A more detailed account of the character of the cells composing these tissues may be appropriately undertaken now, for although all the tissues here mentioned are present in root, stem, and leaf, they reach their greatest differentiation and complexity in the stem, and in this region of the plant they can therefore most profitably be studied. The structure of the fibro-vascular tissues of a woody dicotyledonous plant can well be seen in Figs. 49 and 50, a transverse and a radial longitudinal section through a portion of the stem shown in Fig. 48.

Protective Layers.—The epidermal cells resemble those of the leaf epidermis and require no special comment. In stems which are growing in thickness, however, the epidermis is soon sloughed off and its protective function is assumed by a layer of corky cells formed directly under it and constantly renewed. In these cells the protoplasm soon disappears and the normal

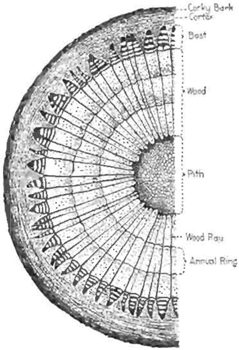


FIG. 48.—Transverse section of a three-year-old twig of the tulip-tree (*Liriodendron*). This is a typical woody twig. The fibro-vascular cylinder consists of a solid ring of wood within and bast without, surrounding a central pith.

cellulose wall becomes corky or *suberized* and is thus rendered almost impermeable to air or water. The lenticels, which we have already mentioned, are spots in this corky layer where the cells are somewhat loose and spongy and thus allow the passage of gases.

Cortex and Pith.—The cortex and the pith are very similar in constitution. Their cells usually remain alive, are roughly spherical in shape, retain their cellulose walls and function chiefly in the storage of food. To such undifferentiated tissues the term *parenchyma* is often applied. In older woody stems the pith often dries up and collapses; and the cortex, crushed by the expansion of the wood underneath it, is finally sloughed off.

Bast.—The fibro-vascular cylinder is composed of two distinct tissues. On the outside is the *bast* or *phloem*, the function of which is to transport the elaborated foods—the carbohydrates,

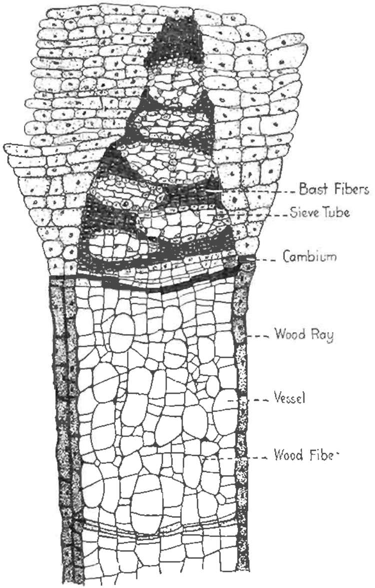


FIG. 49.—Transverse section of wood and bast of the tulip-tree (*Liriodendron*). A portion of Fig. 48 more highly magnified, including part of one of the segments between two wood-rays. The last annual ring of wood, together with one of the groups of bast cells, is included.

fats, and proteins—from one part of the plant to another, especially from regions of manufacture to those of storage or consumption. The cells concerned in this process are the *sieve-tubes* (Fig. 51), living cells with thin cellulose walls but unique

in their lack of a nucleus. They are elongated parallel to the main axis of the stem and their end walls (more rarely their sides) are provided with *sieve-plates* or definite groups of small perforations. Through these perforations extend threads of

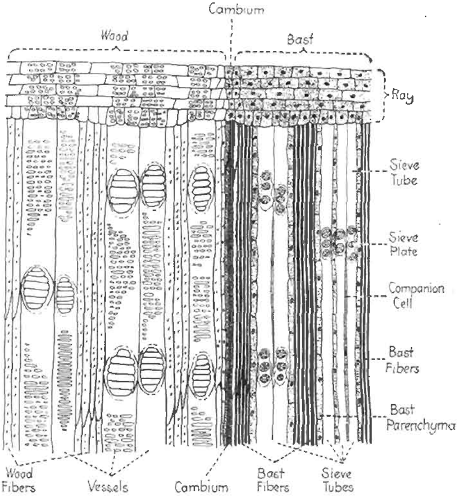


FIG. 50.—Radial longitudinal section of wood and bast of the tulip-tree (*Liriodendron*). Section cut through the region shown in Fig. 49. At the left is the wood, and at the right, the bast, with the cambium between. The ladder-like markings in the vessels are the end walls of the vessel-cells, and the small, elliptical markings are pits in the side walls. The ends of the sieve-tubes are occupied by sieve-plates.

cytoplasm from one cell to another, so that the living substance of each sieve-tube is directly continuous with that of the adjacent ones. In the highest seed plants there is next to each sieve-tube a small *companion cell*, provided with an abundance of cytoplasm and a nucleus. In addition to these two types, groups of long and very thick-walled cells, the *bast-fibers*, characteristically

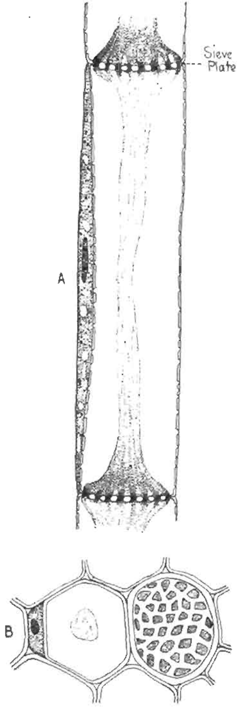


FIG. 51.—The structure of a sieve-tube (Squash). *A*, longitudinal section of a sieve-tube, communicating by sieve-plates with the adjacent sieve-tubes above and below. Its companion-cell is at the left. *B*, transverse sections through two sieve-tubes. The one at the left is cut near the middle. The one at the right is cut near the end, its end wall, or sieve-plate, showing in the section.

occur in the phloem, and some parenchyma is usually present there also.

Wood.—The inner portion of the fibro-vascular cylinder consists of the *wood* or *xylem*, which provides mechanical rigidity for the stem and transports the stream of water and dissolved substances from root to leaf. As essential elements in the xylem

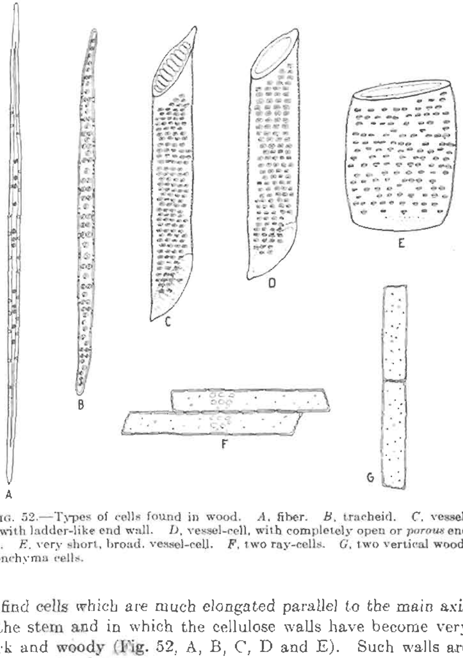


FIG. 52.—Types of cells found in wood. *A*, fiber. *B*, tracheid. *C*, vessel-cell with ladder-like end wall. *D*, vessel-cell, with completely open or *porous* end wall. *E*, very short, broad, vessel-cell. *F*, two ray-cells. *G*, two vertical wood-parenchyma cells.

we find cells which are much elongated parallel to the main axis of the stem and in which the cellulose walls have become very thick and woody (Fig. 52, A, B, C, D and E). Such walls are said to be *lignified*. As soon as one of these cells is fully developed, it dies and its protoplasmic contents disappears, so that only

the thick, woody cell-wall is left. Definite thin areas or *pits* occur at frequent intervals along this wall and facilitate the rapid movement of water. In simpler types of wood, such a cell is able to provide both the necessary rigidity and conductive capacity and is known as a *tracheid*. In the higher types, however, this simple element has become specialized in two directions and has given rise to long and very heavy-walled cells, the *wood-fibers*, in which almost no cavity remains and which contribute a high degree of mechanical strength to the wood; and the *vessel-cells* or *tracheal cells*, much shorter, with wide cavities, and walls which are comparatively thin and are provided with large perforations in their ends. These cells, laid end to end in vertical rows, constitute the *ducts* or *vessels*, so characteristic of the wood of many plants, which carry the ascending stream of water through the stem. Parenchyma cells sometimes occur among the lignified elements and like them may be elongated vertically (Fig. 52, G). Other parenchyma cells are elongated *at right angles* to the stem (Fig. 52, F) and dispersed among the woody cells in horizontal bands or ribbons running out through the xylem along the radii of the stem. These structures are known as the *wood-rays*, and in somewhat modified form extend also into the bast. They facilitate the horizontal transfer of materials in the stem and are of particular importance as centers of food-storage.

Cambium.—A narrow layer of thin-walled cells, the *cambium*, separates the wood from the bast. Through its activity new cells are added to the outside of the wood and the inside of the bast, and the thickness of the stem is thereby increased. Among woody plants, such growth continues from year to year and each season's increment, or *annual ring*, is easily recognizable.

At each node a small but complete segment of the fibro-vascular ring separates from the rest and passes out through the cortex into the base of the petiole, causing a break; or *leaf-gap*, in the ring. Into each leaf may enter one, three, five or more of these *leaf-traces* which are destined to pass upward through the petiole and to form the system of veins in the blade.

Woody and Herbaceous Stems.—The perennial woody stem in which the fibro-vascular cylinder, as seen in cross section, forms a continuous and rather wide ring (except for the leaf-gaps), and which receives additions in thickness year by year through cambial activity, is probably the most ancient stem-type among

seed plants; and the herbaceous condition, where the stems are much softer and shorter-lived, has apparently been derived from it in response to climatic changes or for other reasons. In herbaceous species, the amount of fibro-vascular tissue has become proportionally very much less. This may be due simply to a decrease in the activity of the entire cambium, or to the breaking up of the cylinder into separate bundles, but in general

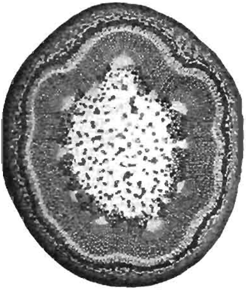


FIG. 53.

FIG. 54.

FIG. 53.—Transverse section of a one-year-old twig of the sweet gum (*Liquid ambar*), showing the continuous fibro-vascular cylinder.

FIG. 54.—Transverse section of a one-year-old twig of the sycamore (*Platanus*), showing the fibro-vascular cylinder broken up into segments by the development of wide rays. (*Figs. 53 and 54 from Sinnott and Bailey*).

any herbaceous stem is roughly comparable to a one-year-old twig of the particular woody stem-type from which it has been evolved. The herbaceous stem in Fig. 55, with its thin but continuous vascular ring, has probably arisen from some such woody form as is shown in Fig. 53, where the vascular ring is similarly continuous and homogeneous. The stem in Fig. 56, however, in which the cylinder has been broken into distinct and completely separate bundles, is quite different in type and has probably arisen from a woody stem somewhat resembling that in Fig. 54, where the vascular ring is divided into segments by the development of very wide rays. Cambial activity is usually weaker opposite these rays than opposite the woody segments of the cylinder, and in the stouter herbs of this type,

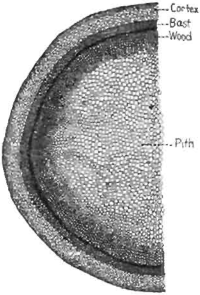


FIG. 55.

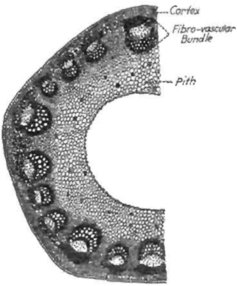


FIG. 56.

FIG. 55.—The stem of an herbaceous plant (*Digitalis*). Transverse section. In this type of herbaceous stem, the fibro-vascular cylinder is thin but unbroken.
FIG. 56.—The stem of an herbaceous plant (*Delphinium*). Transverse section. In this type of herbaceous stem, the fibro-vascular cylinder is broken into a ring of fibro-vascular bundles, each containing a group of wood-cells and a group of bast-cells.

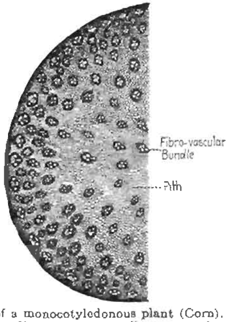


FIG. 57.—The stem of a monocotyledonous plant (Corn). Transverse section, *showing the fibro-vascular bundles scattered in the pith.*

the rays therefore tend to form broad constrictions in the ring. In more delicate herbaceous stems the constrictions finally become complete, the broad rays disappear, and the cylinder is thus broken up into a ring of separate segments or *fibro-vascular bundles*. Each of these consists of a group of wood cells on its inner side and of bast cells on its outer, with a vestige of cambium

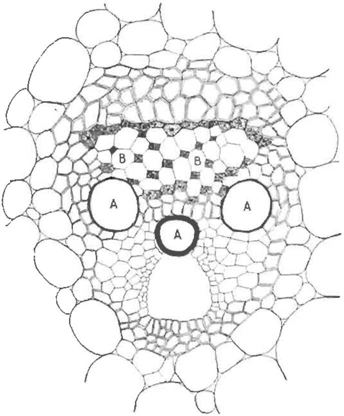


Fig. 58.—Stem-bundle of a monocotyledonous plant. Transverse section of a fibro-vascular bundle from the Corn stem (Fig. 57). *A*, vessels. *B*, sieve-tubes, with companion-cells in their corners. The bundle is surrounded by a *bundle-sheath* of thick-walled cells.

between. Connecting the cambium layers of two adjacent bundles there may be a weak *interfascicular* cambium, producing a few layers of parenchyma cells. In many herbaceous stems, however, the bundles, each surrounded by a *bundle-sheath* of thick-walled cells, are quite distinct and widely separated from one another, with no remnant whatever of a cambial zone between them.

In still more highly specialized stems, characteristic of monocotyledonous plants, the bundles are no longer arranged in a ring but are scattered irregularly throughout the whole area of the

stem (Fig. 57). The individual bundles are very distinctive in appearance (Fig. 58), each possessing a large air-space or *lacuna*, two large vessels, and a patch of very regularly arranged sieve tubes and companion cells. In such a stem no distinction between pith and cortex now remains. The departure of the leaf-traces here is very complex, a large number of bundles moving outward from the center of the stem and entering the sheathing leaf-base.

The Structure of Wood.—In shrubs and trees* the great bulk of the stem, particularly in its older portions, consists of but

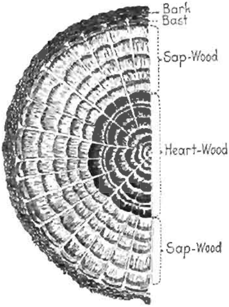


FIG. 59.—Heart-wood and sap-wood. Transversely-cut end of an oak log, showing the darkly-colored heart-wood at the center of the stem, surrounded by the lighter sap-wood.

one tissue, the wood. Wood is so important in the economy of the plant and of such great significance to man that we are justified in studying it a little more closely than we have the other tissues.

Through the activity of the cambium (a fuller account of which we shall reserve for the chapter on growth) a new concentric layer of wood cells is added each year to the outside of the woody cylinder. The tracheids and ducts produced at the beginning of growth in the spring are usually of large diameter and are accompanied by comparatively few fibers, and it is apparently

* Conifers and dicotyledons alone are discussed here. Woody monocotyledons are rare and their woody tissues are very complex.

in this *spring wood* that most of the upward conduction of water takes place. In the later-formed portion of the annual ring, the water-carrying cells are fewer and narrower, and the bulk of the tissue is composed of fibers. This *summer wood* is responsible for most of the rigidity and strength of the stem. In large branches and trunks, the older portion of the wood, consisting of the first-formed annual rings at the center of the stem, in time becomes dead throughout and ceases to perform its functions of

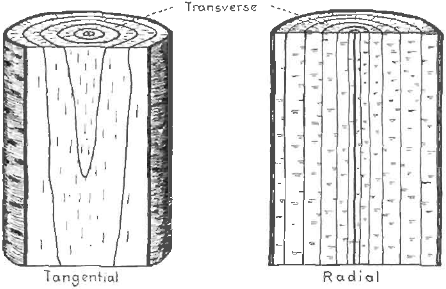


FIG. 60.—Transverse, tangential, and radial sections of wood. Both logs have been cut transversely. In addition, the one at the left has been cut lengthwise tangentially, and the one at the right, lengthwise radially. Each cut presents the appearance characteristic of that particular plane of section. The annual rings and wood rays may be distinguished in all three sections.

water-conduction and storage. It then constitutes the *heart-wood* (Fig. 59) and is frequently distinguished from the outer layers by its darker color. The living and functioning part of the wood is its youngest portion and is known as the *sap-wood* (Fig. 59). This, of course, is on the outside of the woody cylinder, and it is usually rather constant in width in any particular species, its innermost ring being converted into heart-wood each year as its outermost is added by the activity of the cambium. All of the non-woody cells here (the parenchyma cells and ray cells) are alive.

Wood is usually cut along one of three distinct planes, and the cut surface in each case presents a very different appearance (Fig. 60). In describing a given wood it is therefore customary to consider its characteristics as they are shown in these three

cuts or *sections*. An ordinary "cross cut," at right angles to the length of the log, is known as a *transverse* section, and shows the annual rings as a series of concentric circles, with the wood rays running out from the center as narrow lines along the radii. Where the cut is longitudinal and made exactly along the radius of the log, a *radial* section results. This presents the annual rings as vertical straight lines and the wood rays as horizontal

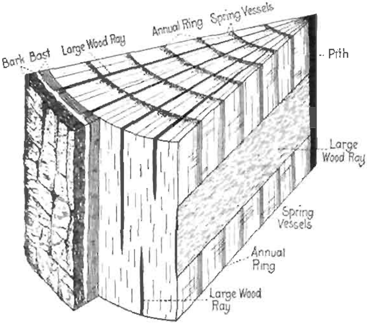


FIG. 61.—A segment of an oak log. At the right, the block has been cut radially, and above, transversely. At the left (the surface of the log) a portion of the bast and corky bark has been removed, showing a tangential view of the wood beneath. The wood rays are narrow sheets of tissue running along the radii of the stem. On the radial face, one of them is shown split open, giving the characteristic "silver grain" of oak wood Between the large rays are many small and narrow ones.

stripes or markings. Where the rays are fairly wide, as in the oak, these markings are prominent and furnish the much-prized "silver grain" so readily seen in quartered oak. Other longitudinal sections, which do not lie in a plane passing through the center of the log, are known as *tangential*. If the structure is exactly regular and the cut exactly true, the annual rings are here seen as straight lines somewhat unequally distant, running up and down along the wood. The irregularities which almost always occur, however, cause the rings in such a cut to appear as wavy lines which produce the common "grain" of most wood surfaces. The rays are very inconspicuous in a tangential section, for only their cut ends are visible. The relations between these

three sections, and the characteristic appearance of the various wood structures as seen in them, is shown in the segment of an oak log (Fig. 61) and the magnified cube of pine wood (Fig. 62).

Woods of various species differ from one another markedly in such gross characters as color, weight, hardness, chemical composition, width of annual rings, width of rays, and number, size

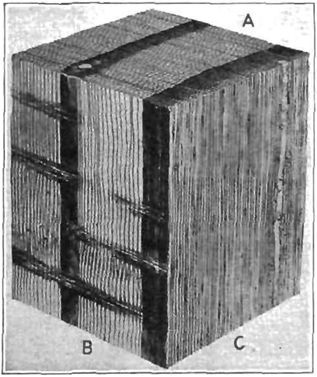
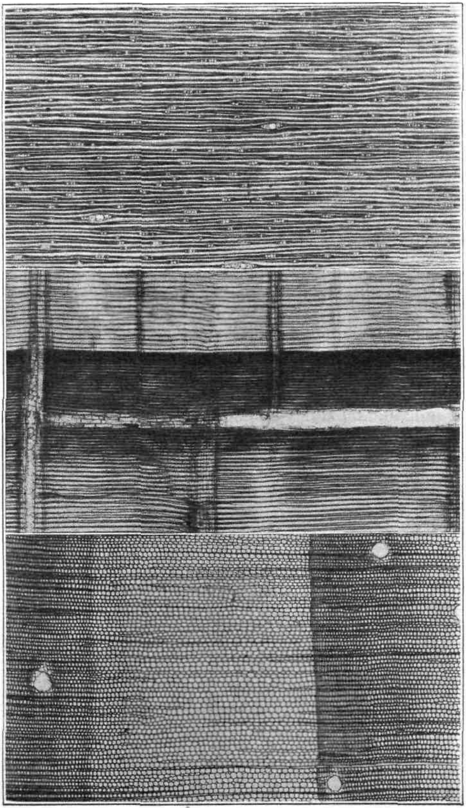


FIG. 62.—Cube of pine wood, much enlarged. *A*, transverse section. *B*, radial section. *C*, tangential section. One entire annual ring and parts of two others are shown. (*Courtesy United States Forest Products Laboratory*).

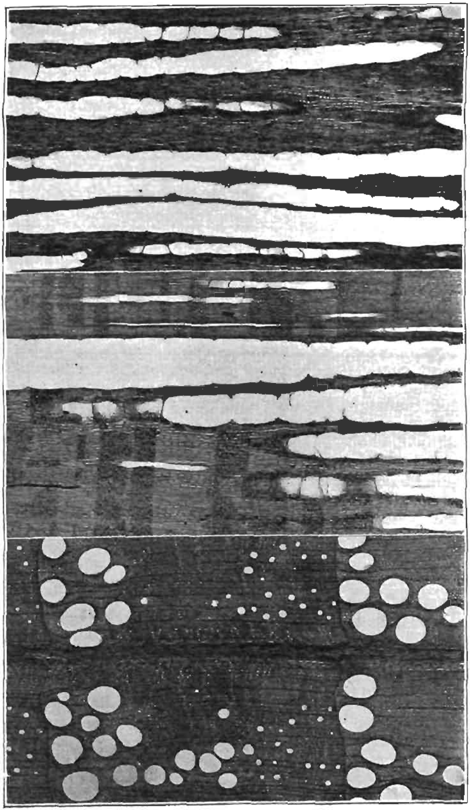
and arrangement of vessels; and in such microscopic features as the size, shape, character, and location of the different classes of wood-elements, the type and distribution of pits, and the various markings on the cell-walls. The structure of two distinct and important woods, those of pine and of oak, are well shown in their transverse, radial and tangential sections in Figs. 63 and 64. The various details of wood structure remain so constant that

FIG. 63.—Pine wood as seen under the microscope. *A*, transverse section. The wood cells (tracheids) are here cut across, at right angles to their length. Note the thin-walled cells in the spring wood and the thick-walled ones in the summer wood. The wood rays run at right angles to the annual rings. *B*, radial section. *C*, tangential section. In both these, the tracheids are cut lengthwise. Note the marked difference in appearance of the wood rays in the three sections. The large openings are resin-canals. (*Courtesy United States Forest Products Laboratory*).



A B C

FIG. 63.



A B C

FIG. 64.

they may often be used to identify the plant species from which a piece of wood has been derived. The great diversity which wood displays, together with its abundance and the ease with which it can be manipulated, have led to its use in numberless ways, and there is consequently no other plant tissue, aside from those used as food, which is of such great economic importance.

The Ascent of Sap in Stems.—We can determine by experiment that water and dissolved substances absorbed by the roots are carried upward in the wood of the stem. As to what causes this movement, however, there is still much question. To explain the ascent of water in low-growing herbaceous plants might be fairly simple, but the factors which bring about the lifting of water in large quantities to the tops of tall trees, sometimes more than three hundred feet above the ground, are very hard to determine. An upward osmotic pull is of course furnished by the increased sap concentration in the leaf-cells which follows the water-loss therefrom in transpiration, but even granting a strong pull at the leaf, the rise obviously cannot be due to simple "suction" or atmospheric pressure. Nor is capillarity probably concerned to any great extent in the process, for, although water may be lifted very high in exceedingly small capillary tubes, its movement is so slow under these conditions that capillarity certainly could not provide the large amounts of water which we know must ascend the trunk daily. Root-pressure, if it were strong enough, might perhaps be important, but root-pressure is manifest in woody plants only during the early spring and is therefore lacking at the season when transpiration is most active. It has been suggested that the living ray and wood parenchyma cells may be concerned in the upward movement of water in some way, perhaps furnishing a continuous series of osmotic pumps. These cells may be of some such service, but we know that for a considerable time, at any rate, water may ascend through a stem where all the living cells have been killed. The most plausible hypothesis yet put forward is based on the very high cohesive power exhibited by water under certain conditions. In very thin water columns, such as must occur in the conducting cells of the

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Fig. 64.—Oak wood as seen under the microscope. *A*, transverse section, showing one complete annual ring and parts of two others. Note the very wide vessels in the spring wood, the narrow ones in the fall wood, the wide wood ray, and the many very narrow ones. *B*, radial section. *C*, tangential section. Note the many differences in structure between this wood and that of pine *(Courtesy United States Forest Products Laboratory)*.

wood, this cohesive power is perhaps so strong that a pull at the top—in this case the osmotic pull at the leaf—will lift the column bodily, as a rope might be lifted. There are certain objections to this explanation, too, but they are not as serious as in the other hypotheses. Possibly several of the factors mentioned may be concerned together in the ascent of sap. We must admit that this problem, like so many others in biology, is as yet far from a satisfactory solution.

The Translocation of Foods.—The plant must possess means not only for insuring the passage of a plentiful supply of water to the leaves through the wood of the stem, petioles and veins, but also for transporting the product of the leaf's activity—the manufactured food in the form of carbohydrates, fats and proteins—to any region of the plant where food is used or stored. This function of translocation is performed chiefly by the sieve-tubes of the bast. The movement of organic substances by diffusion from cell to cell is a comparatively slow process, but is the only means available in regions remote from the vascular system. Movement of food for long distances, as from the leaf to the storage regions of stem and root, seems to take place almost entirely in the bast. Here the protoplasmic connections from sieve-tube to sieve-tube through the sieve-plates do away with the necessity for diffusion through a long series of membranes and thus facilitate the rapid transfer of substances from place to place. This importance of the bast has repeatedly been demonstrated by experiments involving "ringing" or "girdling," in which there is removed from around the stem a continuous encircling strip of tissue, including all bark and bast. It is a *matter of common observation that a tree in which the trunk has* been girdled in this way will ultimately die. Although small in amount, therefore, and rather inconspicuous when compared with the wood, the bast is a vitally necessary tissue in the economy of the plant.

QUESTIONS FOR THOUGHT AND DISCUSSION

334. Most stems tend to be stout below and more slender above. Why is this, and of what advantage is it to the plant?

335. Why are young trees often somewhat spire-shaped but old trees of the same species flat or convex at the top?

336. Does the trunk of a tree become relatively stouter or more slender, compared with the rest of the tree, as the tree grows larger? *Explain.*

337. What difference in method of stem-growth is responsible for the differences in shape between a spruce tree and an elm tree?

338. A group of trees of the same species, growing very close together, will often have approximately the same shape as that of a single, well developed tree. Explain.

339. What advantages and what disadvantages does a climbing plant have as compared with an erect one?

340. What advantages and what disadvantages does a plant with a prostrate stem have as compared with an erect one?

341. What advantages and what disadvantages does an herbaceous plant have as compared with a tree?

342. Trees and shrubs have hard and woody stems, but herbs very much softer ones. Explain.

343. The stems of submersed water plants are very soft and weak. Explain.

344. Give an example of a plant which is practically stemless.

345. By looking at a leafy branch which has been freshly cut from a tree, how can you tell whether it has been growing in a vertical, oblique or horizontal position there?

346. What do you think is the most important function performed by the bud-scales? Explain.

347. Do all the buds on a tree unfold and grow every season? Explain.

348. Why is a potato tuber "morphologically" a stem?

349. Why is it that a woody twig obtains air for its internal tissues through lenticels rather than through stomata, as does a leaf?

350. What is there about the structure of cork which makes it such excellent material for bottle stoppers?

351. What do we mean in saying that the cortex and pith are "undifferentiated" tissues?

352. What is the advantage in having the cells of the conducting tissues much elongated?

353. Wood has a "grain" which in general runs parallel to the axis of the tree. To what is this grain due?

354. Why does wood split easily "with the grain" but not "against the grain"?

355. *What causes knots in wood?*

356. A log otherwise free from knots often shows them near its center. Why?

357. Which will have more and larger knots in its wood, a tree grown in the forest or one grown in the open? Why?

358. Why is the wood of knots apt to be harder than the wood around them?

359. Which will decay faster if exposed freely to the air, heart-wood or sap-wood. Why?

360. By looking at the cut end of a board, how can you tell the position which this board held with reference to the center of the log from which the board was cut?

361. How can you tell whether a piece of furniture is made of veneered wood or not?

362. What two ways do you know for telling the age of a twig?

363. *What makes the annual rings in wood clearly distinct from one another?*

364. What often makes it difficult to count the annual rings of trees which have grown in warm regions?

365. As a tree grows older, which increases more rapidly in thickness, its heart-wood or its sap-wood? Explain.

366. In most woody plants it is only the last year's growth of bast, or at most that of the last few years, which functions in translocating food. Explain.

367. Of what use are the bast-fibers to the plant?

368. What suggestion can you make as to the function of the companion-cells in the bast?

369. How would you prove that the ascending stream of water travels in the wood?

370. Species of trees differ markedly in the height to which they can grow. Can you suggest a factor which may be responsible for this difference?

371. How is it possible for a tree which is "hollow-hearted" to thrive and grow?

372. In tapping maple trees for sap, it is necessary to run the tap into the tree for only a very short distance. Why?

373. Cut flowers will keep fresh longer if the cut ends of their stems are trimmed off daily; if, after cutting, the ends are placed in boiling water for a moment; if the water in which the flowers stand is frequently changed, or if a little salt is added to the water. Explain how it is that these various procedures tend to effect the desired result.

374. How would you prove that manufactured food travels in the bast?

375. Why will a girdled tree ultimately die?

376. Why is the chestnut-bark disease, which attacks only the outer bark, cortex and bast, so fatal to chestnut trees?

377. Why is a wire ring or other tight metal band around a tree trunk likely to injure the tree severely in time?

378. If a trunk is bound tightly with wire, a swelling of the tissues finally appears above the wire. Explain.

379. In propagating a plant by "layering," a gardener bends a branch down to the ground and covers a portion of it with earth in order that it may root at that point. Roots will grow much better if the stem is bent or twisted strongly at the point where roots are desired. Why?

380. In "Chinese" layering, a ring of bark is cut off around the stem, as far in as the wood, and that part of the stem is covered with moist moss. Roots eventually appear just above the ring, but not below it. Explain.

381. In order to obtain very large fruits for exhibition, growers sometimes "ring" a fruit-bearing branch some distance below where the fruit is growing. Explain why this has the desired result.

382. What foundation in fact is there for the old belief that by driving nails into the trunk of a plum or a peach tree, larger fruit will be obtained?

383. If a tree is "girdled" while its leaves are out, will the leaves wilt or not?

REFERENCE PROBLEMS

49. Give an example of a stem which has assumed some of the functions of a leaf; of a root.

50. Why does a gardener use "brush" to support peas but poles to support beans?

51. Do all buds have scales?

52. Give an example of buds which do not arise at a node.

53. Why do apple and elm trunks make better chopping blocks than do most woods?

54. What is the essential feature in the manufacture of wood-pulp?

55. Why is paper that is made from wood-pulp so much less tough than that made from cotton or linen?

56. What is the difference between a wood which is *ring-porous* and one which is *diffusely-porous?*

57. What is the process of veneering wood, and what are its advantages and disadvantages?

58. What is "quartered" oak and why is it more expensive than ordinary oak?

59. Why can oak be quartered to advantage although most woods cannot be?

60. Why cannot the ascent of water in the stem of a plant be explained on the principle of a suction pump?

61. Give the derivation of the following terms and explain in what way each is appropriate:

Node	Cortex	Lenticel
Xylem	Tracheid	Phyllotaxy
Phloem	Cambium	Fibro-vascular

CHAPTER VII

METABOLISM

The term *metabolism*, whether used of animals or of plants, refers to the entire series of chemical changes and processes *involved in the activity of the living organism. It may be* divided roughly into *constructive* and *destructive* metabolism. The former process begins, in plants, with the production of simple carbohydrates by photosynthesis, and is concerned with the construction therefrom of the more complex plant foods and with their storage, their digestion, their assimilation into the living protoplasm, and the growth of new tissues which they make possible. The latter process involves a breaking down of the living substance thus built up, with the consequent production of waste materials and a liberation of the energy which is necessary for the activity of the organism.

Plant Foods. We have already discussed the production of glucose by photosynthesis. Glucose is the basic plant food from which are ultimately derived all others—the more complex carbohydrates, the fats, and the proteins—which support the life of animals and plants.

Before we inquire into the characteristics of these various food types and their mode of origin, however, we should consider just what is implied by the term *food* itself. A broad definition would make "food" include everything taken into the body of the organism which is essential to its life and continued activity. Water, carbon dioxide, and the various essential mineral salts would thus be considered as the food of plants, and indeed it is the last of these which in ordinary speech are most commonly referred to as "plant foods." From such a conception of food as this, however, has arisen a fallacious distinction sometimes drawn between animals and plants, namely that the former require organic food and the latter only inorganic. A more strict and perhaps from our point of view a more useful employment of the term "food" limits its application to anything which supplies either of the two fundamental needs of the organism—

energy and building-materials. We may therefore define food as *whatever furnishes a supply of available energy to an organism or contributes materially to the upbuilding of its tissues.* It is the carbohydrates, fats, and proteins which provide the materials for growth, and which, because of their somewhat unstable chemical composition, contain a supply of potential energy readily utilized by the organism. These are the true foods. The essential mineral salts, which constitute a very small portion indeed of the

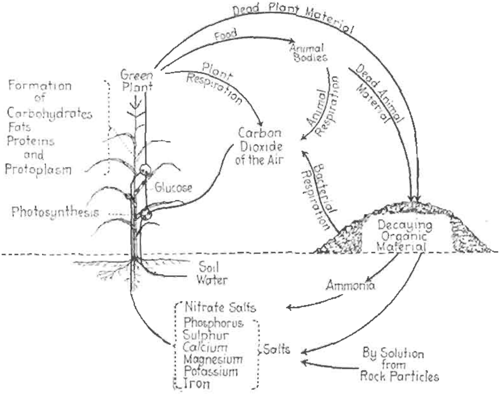

FIG. 65.—The organic food cycle. History of the construction and disintegration of the important organic substances found in plants.

plant body, are neither tissue-builders (except in a very minor degree) nor energy-producers, and hence cannot strictly be regarded as plant foods at all. Their importance lies rather in the fact that they are necessary, in minute quantities, to the construction and successful functioning of protoplasm itself. Together with water and carbon dioxide they may appropriately be called *nutrient materials.*

The food of plants and animals is essentially the same and the difference between the two groups, therefore, lies not in the character of the food which they use but in the fact that green plants are capable of synthesizing food from inorganic nutrient

materials and that animals are not. Given a simple food like glucose, however, both animals and plants are able to construct therefrom an endless variety of more complex foods and of other organic compounds. There is thus a constant circulation of various materials through air and soil and through the bodies of green plants, of animals and of bacteria, a process by which organic substances are continually being built up and broken down. This *Organic Cycle* is graphically represented in Fig. 65.

Foods may be divided into three main classes, which we call *carbohydrates*, *fats*, and *proteins*. These food types differ from each other in physical structure and chemical composition as well as in the parts which they play in nutrition.

A. *Carbohydrates.*—Carbohydrates are substances composed entirely of carbon, hydrogen, and oxygen, in which the hydrogen atoms are about twice as numerous as those of oxygen. Glucose ($C_6H_{12}O_6$), the product of photosynthesis, is an example of a very simple carbohydrate. To this group of foods belong the various sugars, starches, and celluloses, which comprise the great bulk of the food of animals and plants. Carbohydrates are the chief source of energy for all organisms and provide most of the building material for the plant body.

The *sugars* are soluble carbohydrates. Three are more common in plants than others. These are *glucose* or grape sugar, $C_6H_{12}O_6$, the direct product of photosynthesis; *fructose* or fruit sugar, identical in chemical formula with glucose but differing in the arrangement of its atoms and in certain physical characteristics; and *sucrose* (cane sugar or beet sugar), with the formula $C_{12}H_{22}O_{11}$, and produced from the simpler sugars by the removal of a molecule of water, thus:

$$2C_6H_{12}O_6 - H_2O = C_{12}H_{22}O_{11}$$

These three types of sugar are all common in plants, though in any particular species one is usually more abundant than the others. Glucose and fructose form the bulk of the sugar of fruits and of the nectar of flowers, from which honey is derived, and are common elsewhere, glucose probably occurring in every living plant cell. Sucrose is abundant in the sugar-cane and sugar-beet and is therefore the type of sugar with which we are most familiar. Sugars are stored in many plants as reserve foods, but are also widely distributed throughout the plant body, because of the fact that those carbohydrates which are insoluble

must be converted into sugar before they can be transported from place to place, or before they can be assimilated into living protoplasm.

The *starches* are insoluble carbohydrates, derived from glucose but much more complex in their chemical composition. Their general formula is $(C_6H_{10}O_5)_n$. Starch is produced from glucose by the removal of water, thus:

$$nC_6H_{12}O_6 - nH_2O = (C_6H_{10}O_5)_n$$

The formation of starch is confined to certain plastids in the cell. These are the chloroplasts, in cells where photosynthesis is going

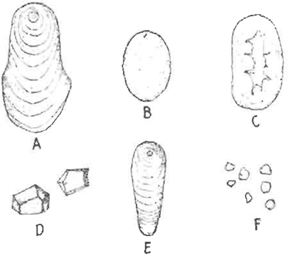

FIG. 66.—Starch-grains from various plants. *A*, potato. *B*, wheat. *C*, bean. *D*, corn. *E*, gloxinia. *F*, rice.

on, and the *leucoplasts* in storage cells. In these plastids the starch is laid down in small grains which increase in number and size until in storage tissues the entire cell-cavity may become filled with them. Starch-grains usually display very characteristic shapes and markings distinctive of the species by which they are produced (Fig. 66). Indeed, it is often possible by this means to identify with certainty the source from which a particular sample of starch has been derived. A definite core or *hilum*, often cracked and shrunken, appears in most cases in the grain and is usually surrounded by a series of more or less concentric rings or striations.

Cellulose is a carbohydrate even more complex chemically and physically than starch but with the same basic formula,

$(C_6H_{10}O_5)_n$. Because of its comparative indigestibility cellulose is not usually available as a food, though in certain plants a layer of it is deposited on the inside of the cell-wall during periods of food-storage and is later absorbed and used by the plant. Such *reserve cellulose* is in some cases an important source of food. Of far more significance than its use as a food, however, is the fact that cellulose is the material out of which the cell-wall, and therefore the entire skeleton of the plant, is constructed.

B. *Fats.*—Fats resemble carbohydrates in being composed only of carbon, hydrogen, and oxygen, but differ from them in the relative proportion of these elements. The hydrogen atoms are approximately twice as numerous as those of carbon, but in comparison with these two, the amount of oxygen is very small. Three common plant fats well illustrate the chemical composition of this type of food. These are palmitin, $C_3H_5(CO_2C_{15}H_{31})_3$; stearin, $C_3H_5(CO_2C_{17}H_{35})_3$; and olein, $C_3H_5(CO_2C_{17}H_{33})_3$. Some fats are liquid and others solid at ordinary temperatures. Fats are insoluble in water and when moved about from cell to cell by diffusion a fat must therefore be broken down into its simpler and soluble components, glycerine and a fatty acid. In nature, fats are readily converted into sugars and sugars into fats. Fats are not as common a type of food as carbohydrates among plants, but are nevertheless of frequent occurrence in certain situations, particularly in seeds and other regions where food in concentrated form is advantageous. They are apparently not produced by any special plastids but appear in the form of minute droplets in the cytoplasm. Fats are chiefly important as sources of energy.

C. *Proteins.*—Proteins are composed not only of the basic carbon, hydrogen, and oxygen of the carbohydrates and fats, but include nitrogen also, and generally a small amount of sulphur. They are exceedingly variable, both in chemical composition and in physical properties, and are often very unstable. Protein molecules are large and complex, as is illustrated by the calculated formulas of two common plant proteins, *zein* of corn, $C_{736}H_{1161}N_{184}O_{208}S_3$; and *gliadin* of wheat, $C_{685}H_{1068}N_{196}O_{211}S_5$. We know less about proteins than about any other class of organic compounds. They are of particular interest from the fact that protoplasm itself is a mixture of complex proteins.

Proteins undoubtedly are formed by the union of a simple carbohydrate, such as the glucose which has been produced in

photosynthesis, with nitrogen and sulphur which have been taken into the plant from the soil through the root-hairs. This union probably occurs most commonly in the leaves. It is a noteworthy fact that (with a few exceptions) plants alone seem to possess the ability to bring about this synthesis of protein, an ability almost as significant to the rest of the organic world as is that which enables them to manufacture carbohydrates from inorganic substances. Animals depend almost entirely upon plants for their supply of proteins. If given the simple protein compounds, however, animals can build therefrom new and characteristic protein materials of all kinds.

Proteins, with their highly complex molecules, are not produced directly but are built up by an aggregation of simpler nitrogenous compounds, the *amino-acids*, which have been called their "building-stones". Over twenty of these compounds have been isolated and studied. Among these are *glycine*, $C_2H_5NO_2$; *leucine*, $C_6H_{13}NO_2$; *glutamic acid*, $C_5H_9NO_4$; and *tryptophane*, $C_{11}H_{12}N_2O_2$. From these amino-acids, with the addition of sulphur, are constructed all the proteins in almost infinite variety, —the *albumins, globulins, glutelins, prolamins*, and many others, which differ in composition, solubility, stability, and other respects.

Most of the protein which is stored as a reserve food in plants occurs in definite bodies, the *aleurone-grains*, which are secreted by the protoplasm much as are starch-grains and which often fill the sap-cavity. The storage of proteins in this form is frequently confined to particular regions of the plant. Thus the *aleurone layer* of cereal grains, a single layer of cells just under the pericarp, is filled with aleurone and is thus rich in protein.

Proteins are much less abundant as reserve foods than are carbohydrates, and are relatively poor energy-producers, but their composition makes them far more effective than any other foods in the construction and renewal of living substance. As "tissue-builders" proteins therefore play a vital part in the nutrition of plants and animals.

Digestion.—We have already seen that the physiological processes of a plant are concerned almost entirely with substances which are *in solution*, and that in order to enter the plant body from the soil or the air or to pass from one cell to another within it, a substance must first be dissolved. Insoluble materials are of little significance in the economy of protoplasm. Most of the

food substances which we have discussed above exist commonly in forms which are not soluble in water. The advantages of this in the storage of reserve foods is obvious. It is evident, however, that before such foods can be moved or *translocated* within the plant, and before they can be assimilated into living protoplasm, they must in some way be made soluble; and it is this process of converting an insoluble food into soluble form which is known as *digestion*.

Digestion is brought about through the activity of certain highly important but little understood substances known as *enzymes* or *ferments*. Enzymes are concerned not alone in digestion but in the production of many other chemical changes in the plant. They occur in great variety and are probably protein in character, although their composition is not definitely known. Enzymes are usually present in exceedingly small quantities but are able to effect profound chemical changes out of all proportion to their bulk. How they do this we do not understand. The enzyme apparently does not enter into the composition of the substance produced, nor does it contribute energy for the process, and it is not consumed or used up. It seems merely to hasten a chemical reaction which might still take place, although very slowly, in its absence. Enzymes have thus been said to "lubricate" reactions. Temperature largely controls their rate of activity, each enzyme having an optimum temperature at which it works most rapidly. These remarkable substances may be destroyed by heat and even by certain poisons. Aside from effecting digestion, they are concerned with the changes which take place in the various fermentations and in decay; with the process of oxidation in living tissues, and with the synthesis and decomposition of many organic substances. Indeed, most of the metabolic processes of plants and animals are probably dependent, in one way or another, upon enzymes.

It is only the digestive enzymes and their activities with which we are here concerned. Digestion is generally accompanied by *hydrolysis*, or the addition of one or more molecules of water to a molecule of the substance to be digested. The sugars are soluble and most of them may be assimilated directly without digestion. Cane sugar, however, is often broken down into glucose and fructose through the agency of the enzyme *invertase*, thus:

$$C_{12}H_{22}O_{11} + H_2O = 2C_6H_{12}O_6$$

Maltose is also converted into glucose by *maltase*. Far more important than these changes, however, is the digestion of starch through the action of *diastase* and other enzymes, with the ultimate production of glucose, thus:

$$C_6H_{10}O_5 + H_2O = C_6H_{12}O_6$$

The reserve celluloses are broken down by hydrolysis into various sugars through the action of another enzyme, *cellulase*. Fats, by the agency of *lipase* and similar enzymes, are broken into glycerine and fatty acids, which may be absorbed into protoplasm. Protein-digesting enzymes are necessarily numerous, but two of them, *pepsin* and *trypsin*, are especially important. The former converts proteins into water-soluble peptones and proteoses; the latter carries the process still further with the ultimate production of amino-acids. It should be noted that all these types of digestion are carried on within the protoplasm of living cells throughout the plant body wherever digestion is necessary, and not in the cavities of special digestive organs.

Assimilation.—After a food has been digested, it must then enter the protoplasm of a cell and become an integral part of the living substance. About this process, which is known as *assimilation* and which is really the central problem of metabolism, we know very little. From the activities of protoplasm it is clear that this remarkable substance must be very complex, both chemically and physically. It is highly unstable and is continually undergoing processes of construction and destruction. Although we can trace with some confidence the entrance into protoplasm of certain comparatively simple substances and the departure therefrom of others equally simple, we must plead almost complete ignorance as to the happenings which take place between these two events. It is here that dead matter becomes alive, that inert food substances become endowed with those unique properties of protoplasm which in the aggregate we call *life*. This change never occurs spontaneously in nature, but is always brought about through the activity of living substance already existing. As far as experience tells us, life always comes from life and in no other way. Although this process is going on continually in every living plant and animal, we have as yet been quite unable to master its intricacies and to imitate it in the laboratory.

Respiration.—Hitherto we have been considering those physiological changes which involve the progressive building up and elaboration of organic materials, a constructive process which reaches its climax in the production of protoplasm. This constant upbuilding and renewal of the living substance is succeeded by an equally constant process of disintegration, which results in the liberation of energy and which is usually accompanied by the intake of oxygen and the outgo of carbon dioxide. To this general process the name *respiration* has been given.

Before we enter upon a detailed study of this important phase of plant physiology we should discuss briefly the problem which it brings up, namely the *energy-relations* of the plant, of which the processes of food synthesis and nutrition form an essential part. Like every living thing, the plant is continually active. This activity shows itself in movement of various sorts, either of the plant body as a whole, of the substances within it, of the atoms and molecules during those chemical changes which are always taking place in living cells, or in the phenomena of growth. These various movements, the maintenance of which is necessary if the plant is to remain alive, require the expenditure of *energy*, as do any movements of matter; and one of the chief problems in the economy of the plant, as in the operation of a machine, is to obtain an adequate supply of energy and to liberate it at the proper times and in the proper places.

Kinetic and Potential Energy.—Energy exists in the universe in two forms: Active or *kinetic* and stored or *potential* energy. Kinetic energy performs work by setting matter in motion, sometimes by changing its position, sometimes by raising its temperature, sometimes by producing chemical alterations within it, and sometimes in other ways. Potential energy is inactive energy, stored up in an object by virtue of the position or condition of that object. Potential energy exists in a stretched spring, in a bent bow, in the water of a mountain stream, in a charged battery, in a piece of coal, or in an explosive. It is present in an object *only as the result of the previous expenditure of kinetic energy upon that object.* Care should of course be taken not to confuse this "storage" of energy with the storage of food or any other form of *matter*. The presence or absence of a supply of stored energy in a given body merely affects the relations between its parts and does not alter in the least the bulk of the object or the amount of matter which it contains. We need

only to remember that a bent spring weighs no more than an unbent one or a charged battery than an uncharged one. Energy and matter are fundamentally distinct.

Release of Stored Energy.—The potential energy in an object may at any time, under an appropriate stimulus, become converted again into kinetic form and do work, as when the stretched spring moves the mechanism of a watch, the bow moves the arrow, the falling water moves a mill wheel, the battery moves a telegraph sounder, the burning coal converts water into steam which moves a machine, or the explosive moves a projectile. In all of these cases the supply of stored energy is finally exhausted and motion ceases. In this process of converting kinetic into potential energy and back again, *no energy is gained or lost, the total amount remaining constant.*

A machine is anything which controls and directs the expenditure of energy so that work of a particular kind is done at a particular place and time. One of its prime necessities is an ample supply of potential energy, and in the machines with which we are most familiar this is available in the form of wood, coal, oil, or stored electricity. The living organism resembles a machine in the fact that it, too, directs the expenditure of energy, and it therefore needs a plentiful supply of this energy in potential form which it may liberate, in the process of respiration, at any point throughout its body for the performance of its many activities. The fuel which the organic machine uses in this process we know as *food*, and the potential energy within this food came originally from the kinetic energy of sunlight and was converted into potential form by photosynthesis in the green cells of the leaf. Food resembles wood, coal, or oil in being a somewhat unstable chemical compound which, through the addition of oxygen, will rapidly break down and resolve itself into simpler components, usually carbon dioxide and water, and thus release the potential energy it contains. This process of *oxidation* is common in nature. In ordinary fuels it takes place only at high temperatures and is then known as *combustion*. In living organisms it can go on at much lower temperatures and is here known as physiological combustion or respiration. In their essential feature—the liberation of energy in kinetic form by the breaking down of complex and unstable chemical compounds into simpler ones through the addition of oxygen—respiration and combustion are precisely similar.

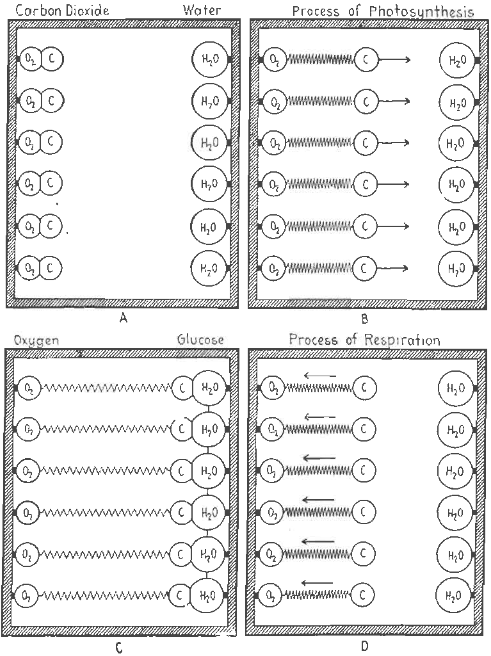

FIG. 67.—The energy relations of photosynthesis and respiration. Diagram showing the operation of a simple laboratory model. *A*, six molecules of carbon dioxide and six of water, the raw materials for photosynthesis. *B*, photosynthesis. By the kinetic energy of light, the molecules of carbon dioxide are broken up and the carbon atoms are being pulled over and attached to the water molecules, thus stretching the six springs which unite the carbon and oxygen. *C*, the products of photosynthesis, a molecule of glucose and six of oxygen. The energy exerted in photosynthesis is now stored in potential form in the glucose molecule (actually, of course, in the stretched springs). *D*, respiration. The potential energy in glucose is being released in kinetic form (by the contraction of the springs) in respiration, as the result of which the atoms are again arranged as six molecules of carbon dioxide and six of water. This, of course, is a very crude imitation of the processes involved and should not be interpreted too literally.

A machine is supplied with fuel (its "food") by an operator, and an animal obtains its food by seizure, but the food which a green plant consumes must be secured through the plant's own activities. The significance of the food-making process we call photosynthesis is now more evident than before. The kinetic energy which the plant, through its chlorophyll, absorbs directly from the rays of the sun is here used to do the work of pulling together carbon dioxide and water and uniting them into the simple food glucose (Fig. 67). The energy expended in accomplishing this union is obviously stored up in potential form in the molecules of the glucose and of the other foods or plant materials which may be derived therefrom, just as the energy expended in winding a clock is stored up in the compressed mainspring. Under appropriate conditions this potential energy may be liberated anywhere and at any time to do work in any organism. One of the most important principles of physiology is thus brought out—that food is merely the medium by which energy received from the sun intermittently and only in certain exposed organs is stored up, carried to all parts of the plant, and made available for work at all times and in all places. This conception has been concisely formulated in the metaphor that "food is a 'storage battery,' charged in green leaves by the sun and discharged in the body by respiration".

The Importance of Photosynthesis.—The importance of photosynthesis to the organic world lies in the fact that this process is practically the only means whereby living things can store up energy. Green plants, the ultimate providers of all foods, are the sole agencies through which the animals and man can tap the abundant supplies of energy in the universe and obtain therefrom a sufficient quantity to maintain their varied activities. This energy is all stored originally in the molecule of glucose, and before it is converted again into kinetic form may pass through scores of modifications and enter into the composition of the bodies of a dozen successive organisms. Although kinetic energy is streaming upon the earth daily in untold quantities from the sun, only the chlorophyll-bearing plants are able to use it directly. Even in industry, man still depends very largely upon photosynthesis, since the energy which he releases from wood, coal, and oil was originally locked up in these substances, in some cases millions of years ago, by the photosynthetic activity of green plants.

Respiration and Life.—With an understanding of the significance of the plant's energy relationships and the part which respiration plays therein, we may pass to a more detailed study of respiration itself. This process, unlike photosynthesis, is not carried on in particular organs and under particular conditions, but is universal, taking place under all conditions and in *every living cell.* Respiration, indeed, is believed to be a necessary accompaniment of life itself, as might be inferred from the fact that living protoplasm is continually active and is thus continually expending energy. Even in cells which are dormant and show no external signs of life, respiration, though very feeble, may still be detected. The amount of respiration which takes place is a rough index of the activity of the cell, organ, or organism studied.

The liberation of energy is the essential feature of respiration and the addition of oxygen is its usual accompaniment, particularly in the higher plants; but in certain cases and under certain conditions, notably among some of the lowest members of the plant kingdom, respiration may be carried on in the absence of oxygen. These two types we recognize as *aerobic* and *anaerobic* respiration. They are so different as to require separate consideration.

Aerobic Respiration.—Aerobic respiration is essentially an oxidation process. Free oxygen is added to organic substances (chiefly carbohydrates) with the consequent breaking down of the latter into their original inorganic components, carbon dioxide and water, thus.

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$$

The oxygen is usually taken directly from the atmospbere through stomata, lenticels, or other openings.

This process of oxidation is one of those chemical changes which are assisted by enzymes, and the oxidizing enzymes or *oxidases* occur in every living cell. As to whether it is the *protoplasm itself* or *unassimilated food substance* within the protoplasm which is oxidized, there is some difference of opinion. It is certain, however, that most of the carbohydrates and fats which are taken into the protoplasm soon furnish, either directly or indirectly, the material which is oxidized in respiration. Proteins, although their chief function is constructive, undoubtedly also contribute to the supply of oxidizable substances. Whatever nitrogenous waste material is given off in their dis-

integration, however, must immediately be assimilated again, for (at least among the higher plants) nitrogenous compounds do not appear among the products of respiration.

Carbon dioxide is almost invariably a product both of aerobic *and of anaerobic respiration. Indeed, the evolution of this gas,* even in minute amounts, is regarded as proof that the organism is respiring and therefore alive. The amount of oxygen taken in and the amount of carbon dioxide given off are in the long run equal, though under certain conditions one may temporarily exceed the other.

Much of the energy liberated in respiration ultimately appears as heat, and a respiring organism will therefore tend to raise the temperature of its surroundings.

By *comparing the chemical equations for photosynthesis and* aerobic respiration, it will be seen that one is the precise reverse or reciprocal of the other. Photosynthesis adds carbon dioxide to water and produces sugar and oxygen. Respiration adds oxygen to sugar and produces carbon dioxide and water. These two processes may actually be going on in the same tissue at the same time, a circumstance which has made the study of plant metabolism peculiarly difficult, since one activity may mask the other. Photosynthesis, however, is confined to the chlorophyll-bearing cells and occurs in them only in the presence of light. In such cells there is a preponderance of photosynthesis in the daytime and of respiration at night. For a brief period in the morning and again at night, and for longer times when illumination is low or other conditions unfavorable for photosynthesis, the two processes may balance each other exactly, the tissues giving off in photosynthesis just the amount of oxygen which is necessary to carry on their respiratory activity. Respiration, unlike photosynthesis, occurs in every living cell.

Comparison between Photosynthesis and Aerobic Respiration.—A brief comparison between photosynthesis and respiration is presented in tabular form below:

PHOTOSYNTHESIS	RESPIRATION
Stores energy	Releases energy
Absorbs carbon dioxide	Liberates carbon dioxide
Liberates oxygen	Absorbs oxygen
Takes place only in green plants	Takes place in all plants and animals
Takes place only in chlorophyll-bearing cells	Takes place in all living cells
Constructs food	Destroys food
Increases weight	Decreases weight.

In its essential characteristics—intake of oxygen, liberation of energy and raising of temperature—the aerobic respiration of plants is exactly comparable to the respiration of animals, a fact which the complexities of plant metabolism sometimes obscure.

Anaerobic Respiration (Fermentation).—Anaerobic respiration, in which the breaking down of chemical compounds and the consequent liberation of energy is not accompanied by an intake of free oxygen, is characteristic of certain lowly plants and sometimes of higher ones when temporarily deprived of oxygen. The best known examples of this process are alcoholic fermentations and allied phenomena. These were named "fermentations" from the fact that the activity of ferments (now more commonly called enzymes) was here first clearly shown. There is consequently a confusion in the application of the term *fermentation*, the commonest usage regarding it as practically synonymous with anaerobic respiration, the other expanding it to cover all activity brought about by the agency of enzymes.

The most important characteristic of anaerobic respiration is the fact that it does not lead to a complete breaking down of the organic substance or food but only to its partial decomposition, with the result that a quantity of more or less complex by-products is formed which still contain a considerable amount of potential energy. The accumulation of these by-products often stops the process itself.

The fermentation of sugar by yeast is the classic example of anaerobic respiration. The yeast plants—minute, single-celled organisms—thrive in rather weak solutions of sugar. Those which have easy access to the air usually respire aerobically, but if the supply of free oxygen is limited (as is the case anywhere below the surface of the liquid) or if it becomes exhausted, the yeast respires anaerobically. The cells now obtain their energy through a *partial* decomposition of the sugar, with the formation of carbon dioxide and a complex by-product, ethyl alcohol, thus:

$$C_6H_{12}O_6 = 2CO_2 + 2C_2H_5OH \text{ (alcohol)}$$

This change is effected by the activity of an enzyme, *zymase*, which is secreted by the yeast cells. It is evident that only a portion of the potential energy in the sugar has been liberated, for the resulting alcohol may be absorbed by another organism, or may be burned, and will then yield a considerable amount of additional energy. When the concentration of alcohol has reached

a certain point, it poisons the yeast plant and fermentation ceases.

The respiration of other minute plants may also bring about alcoholic fermentation, and still others produce fermentations

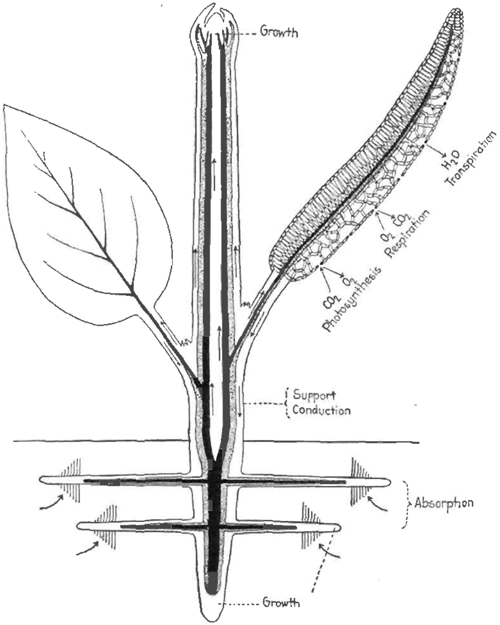

FIG 68.—Important structures and functions of the plant. Diagrammatic representation of roots, stem, leaves, and buds and their functions. Wood solid black, bast dotted, pith and cortex white. Arrows indicate movement of materials into the plant, along the stem, and to and from the leaves. One leaf represented in section. Water passes from the root upward to stem and leaves, through the wood. Manufactured food passes from the leaves both upward and downward, through the bast. The various gas-exchanges between leaf and atmosphere are graphically represented.

of different types, such as those having for their by-products butyric acid (in the spoiling of butter), lactic acid (in the souring of milk), and various others, many of which are of economic importance.

In all these cases energy is liberated and may be detected by the consequent rise in temperature, which is often more marked than in aerobic respiration.

Certain micro-organisms are exclusively anaerobic and are actually killed by the presence of free oxygen. Others, like yeast, may respire either aerobically or anaerobically, depending upon the external conditions.

The decay of dead organic matter is due almost entirely to the respiration of micro-organisms. If the material is exposed freely to the air, bacteria will break it down rapidly and completely by their aerobic respiration. If free oxygen is unavailable, as is the case within a large mass of dead organic material, the process is carried on anaerobically and is slower and more complicated. Here a whole series of micro-organisms, each specific in its activity, are successively concerned. One type will break down the organic substance partially, extracting a certain amount of the potential energy which it contains. In its altered chemical state and with its diminished supply of energy, the remaining material is now seized upon by another type of micro-organism and, entering into the anaerobic respiration of this form, is still further broken down and loses still more of its potential energy. This process continues until finally the whole of the material (except its mineral constituents) passes into the atmosphere as carbon dioxide, water and nitrogen, the original materials out of which organic substance is constructed.

We have now completed a study of the root, the stem, and the leaf, and of the functions of absorption, conduction, photosynthesis, respiration, and transpiration. These are the main vegetative structures and functions of the plant body, and are graphically set forth in Fig. 68.

QUESTIONS FOR THOUGHT AND DISCUSSION

384. Which of the three main types of food makes up the largest part of the diet of animals and man?

385. What advantage is it to the plant to have its carbohydrate food stored chiefly in the form of starch rather than chiefly in the form of sugar?

386. What is it that makes fats the most concentrated of foods?

387. Why are proteins "far more effective than any other foods in the construction and renewal of living substance"?

388. Crops belonging to the Legume family usually contain more protein than most crops. Explain.

389. Where and when in a plant does digestion take place most *vigorously?*

390. What important difference is there between the process of digestion in plants and that in animals?

391. Just how does food which is stored in the endosperm of a seed, and which is therefore not in the young embryo plant itself, become available to this young plant?

392. In what way do the insects captured by an insectivorous plant become available to it as food?

393. Why do parsnips taste so much sweeter in the early spring than in the previous fall?

394. Why are vegetables like peas and sweet corn much sweeter in their young and immature state than when they grow older?

395. Maple sap is very sweet in the spring but contains almost no sugar in the summer. Explain.

396. Hay harvested before its seed is ripe has much more feed value than it has a few weeks later. Why?

397. Certain fungi attack wood, their very delicate, thread-like branches penetrating readily into the hard, woody tissues. How is it possible for them to do this?

398. Give three examples from every-day life (aside from those mentioned in the text) of the conversion of kinetic into potential energy and its subsequent release in kinetic form again.

399. What is the ultimate source of all energy liberated in the bodies of plants and animals? Explain.

400. Just where in the plant body is kinetic energy changed into potential energy and just where is potential energy changed into kinetic?

401. What was the original source of the energy which we derive from the burning of wood? Explain.

402. What main sources of energy used by man in his industries owe their origin to photosynthesis? What do not?

403. Is photosynthesis or respiration the more active process in a normal green plant? How do you know this?

404. Why is an excretory system, so necessary in animals, not needed in the case of plants?

405. State all the resemblances you can think of between an organism and the flame of a candle.

406. How is it possible for oxygen to get into a living cell?

407. How do you think oxygen penetrates to cells deeply seated in the plant body?

408. Through what structures does oxygen enter (1) a young, growing root, (2) a leaf, (3) a woody twig, and (4) an old trunk?

409. How do submersed water plants get their supply of oxygen?

410. Plants which live in bogs or very wet places usually have large air chambers in their tissues, particularly in roots or other subterranean parts. Explain.

411. Do you think that growing plants are good things to have in a sick-room? Explain.

412. If a plant were to be grown in air which had been freed of oxygen, would it live longer in darkness or in light? Why?

413. A seedling plant which has sprouted and grown in a dark place will have a dry weight which is less than that of the seed from which it grew, although the bulk of the seedling is far greater than that of the seed. Explain.

414. Does the increase in the dry weight of a plant measure the amount of photosynthesis which has taken place in it? Explain.

415. Which of three identical wooden posts will remain sound longest: One left freely exposed to the air, one driven into the soil (as a fence post), or one driven under water (as a pile)? Explain.

416. Most of the fossils of animals and plants which have come down to us were preserved in swamps rather than on high ground. Explain.

417. Why is it necessary to change the water in an aquarium frequently if animals are living in it alone, but infrequently, if at all, when green plants are living in it alone?

418. Where in a plant will you be likely to find the highest temperature?

419. The internal temperature of plants is not far from that of their surroundings; in the higher animals it is usually much above that of their surroundings. Explain.

420. Why do land animals need to have lungs for inhaling and exhaling air, when such structures are unnecessary in plants?

421. Which will weigh more, a piece of sound wood or a piece of decayed wood of the same volume? Which will yield more heat when burned? Explain.

422. Why do plants in glazed pots grow poorly?

423. Why should pebbles or bits of broken pottery be placed in the bottom of a flower pot in which a plant is to be grown?

424. In propagating a plant by "cuttings", a small shoot is cut off and the cut end placed in damp soil, where it takes root. Sand is much better than a heavy clay soil for this purpose. Why?

425. Cut flowers will keep longer in a refrigerator than at ordinary room temperatures. Why?

426. In cranberry bogs which have been flooded in the fall to protect them from frost, the unripe berries suffer much more from "smothering," due to lack of oxygen caused by the flooding, than do the mature, fully ripe ones. Why?

427. Fermentation often generates a considerable gas pressure, but respiration does not. Explain this difference.

428. What causes yeast bread to "rise"?

429. Why is it important to boil down maple sap as soon as it is drawn from the tree rather than to let it stand?

430. When jars of preserved fruit "spoil," why do the covers sometimes blow off?

431. A foundation of stable manure under a hot-bed will "heat" and thus keep the soil warm. Explain.

432. Why must the manure under a hot-bed be moist before it will "heat"?

433. Give at least two reasons for lifting the glass from a hot-bed in the middle of a sunny day?

434. What danger is there in putting insufficiently dried hay into a barn? Explain.

435. The danger mentioned in the previous question is much less if the hay is sprinkled liberally with salt and if the barn is very tightly built. Explain.

Note.—A silo is a large, tank-like structure, open at the top. Green and living corn plants, chopped up into small pieces, are packed tightly into the silo in the fall and fed to cattle during the winter.

436. What prevents the contents of a silo from decaying?

437. During the first few days after a silo is filled, its contents becomes distinctly warm and then gradually cools off. Explain.

438. Why is it necessary to have the walls of a silo built very tightly?

439. If the contents of a silo is not packed down tightly, it is apt to spoil. Why?

440. Why does the upper layer in a silo usually decay?

REFERENCE PROBLEMS

62. Give an example of a plant rich in starch; in fat; in protein.

63. Which will produce more energy per unit of weight, a carbohydrate or a fat? Why?

64. Does fat play a more important part in animal or in plant nutrition? Explain.

65. Why does a starchy food keep better than a fatty one?

66. In general, how are "organic" substances to be distinguished from "inorganic" ones? Why were these terms chosen?

67. By what means does sugar become converted into starch?

68. Explain just what has been the history of a piece of coal and why it produces so much energy when burned.

69. What non-gaseous and unusable waste products sometimes result from plant metabolism, and what does the plant do with them?

70. Do plants ever derive energy from the oxidation of other compounds than those of carbon?

71. Give the derivation of each of the following terms and explain in what way it is appropriate:

Metabolism	Enzyme	Respiration
Digestion	Assimilation	Fermentation

CHAPTER VIII

GROWTH

We have learned that food provides the plant with the energy needed to carry on its various functions. A large part of the food which the plant manufactures is therefore either broken down directly by respiration, to liberate energy for immediate use, or is stored up to meet requirements of this sort which may later arise. A healthy plant, however, produces more food than is necessary to maintain the activities of its living substance, and the surplus may be built into the tissues and used to produce new protoplasm and new cell walls, thus promoting the *growth* of the plant body. Growth represents the excess of constructive over destructive metabolism. A knowledge of just what it involves, and of just how it takes place, is evidently necessary if we are to arrive at a clear understanding of the structure and development of the plant body.

The term "growth", in its simplest usage, refers to any *increase in size*, either of the whole organism or of its parts. This expansion may be a mere swelling brought about by a vigorous absorption of water, or it may be due to an increase in bulk of actual plant material—protoplasm and the dead structures secreted by it. All early stages in growth are of the former type, and the swollen and succulent tissues thus produced gradually attain to normal firmness through the deposition within them of large amounts of new material. Indeed, early growth may be accompanied by an actual, though temporary, decrease in dry weight.

In studying this process of growth in the plant as a whole we must remember that the plant body is made up of a mass of minute cells. The size of the cells in any particular tissue and within the same species is rather constant, and is believed to approximate the size which is most efficient for that particular tissue. Very large cells and very small cells would evidently possess many disadvantages. It is therefore clear that growth must consist in the production of more cells rather than in the

enlargement of those already present; and the method by which new cells are formed and added to the plant body deserves careful study in a consideration of the growth process.

The Production of New Cells.—In the previous discussion of the plant cell (Chapter IV) we noted that it consists of a small mass of living substance or protoplasm in which two parts may be distinguished, the undifferentiated *cytoplasm* and the denser

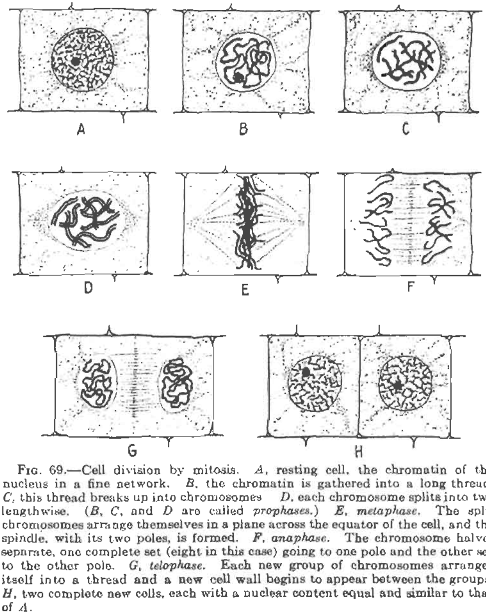

Fig. 69.—Cell division by mitosis. *A*, resting cell, the chromatin of the nucleus in a fine network. *B*, the chromatin is gathered into a long thread. *C*, this thread breaks up into chromosomes *D*, each chromosome splits into two lengthwise. (*B*, *C*, and *D* are called *prophases*.) *E*, *metaphase*. The split chromosomes arrange themselves in a plane across the equator of the cell, and the spindle, with its two poles, is formed. *F*, *anaphase*. The chromosome halves separate, one complete set (eight in this case) going to one pole and the other set to the other pole. *G*, *telophase*. Each new group of chromosomes arranges itself into a thread and a new cell wall begins to appear between the groups. *H*, two complete new cells, each with a nuclear content equal and similar to that of *A*.

and more or less spherical *nucleus*. About the whole is a cellulose wall, deposited by the living substance within much as a clamshell is deposited by the living clam. In growing tissues where

cell multiplication is rapidly going on, the wall is very thin, and the sap cavity, so conspicuous in mature cells, is absent. In the formation of new cells in such growing regions three main stages may be distinguished: *Cell division*, in which the number of cells is increased by the division of each parent cell into two; *cell enlargement*, in which these new cells expand rapidly to their

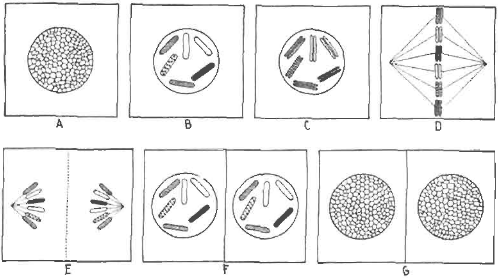

FIG. 70.—Diagram of mitosis in an ordinary body-cell. *A*, resting nucleus. *B* and *C*, prophases. *D*, metaphase. *E*, anaphase. *F*, telophase. *G*, new cells. The separate chromosomes, each of which has an individuality of its own, are differently marked. It is evident that the chromatic material is divided exactly evenly between the two daughter cells. (*Modified from Sharp.*)

final size, and *cell maturation*, in which they assume their mature structure and characteristics (Fig. 71).

Cell Division.—Cell division, technically known as *mitosis*, is not in most cases a simple splitting into two of the mother cells but is accomplished in a rather complex manner (Figs. 69 and 70). The most active part in the process is played by the nucleus. Within this body is a characteristic granular material which stains very deeply with certain dyes used in microscopical work and has hence received the name of *chromatin*. In an ordinary mature cell the chromatin is arranged in a fine network, but when the cell is preparing to divide, the elements of the chromatin network come together into thread-like or rod-like masses, the *chromosomes*. The number of chromosomes is the same in every vegetative cell of the plant and is constant for any particular species. Thus in Indian corn the chromosome number is 20, in wheat 16, in peas 14, and in tobacco 48. Soon after the

chromosomes become evident, two *poles* or apparent centers of attraction, arise in the cytoplasm on opposite sides of the nucleus, and from each of these poles a *spindle* of delicate fibers radiates inward toward the nucleus. The nuclear membrane now disappears and the chromosomes become grouped in a plane or *plate* stretching across the center of the cell at right angles to the two series of spindle fibers, which soon meet and form one continuous spindle reaching from pole to pole. At this point each chromosome has become split lengthwise into two daughter chromosomes, one of which now moves toward one pole and the other toward the other pole. The whole chromatin mass is *thus divided exactly into two and the halves separate widely. Each chromosome group now becomes broken up again into a* network around which a new membrane forms, and two complete nuclei are thus produced. Meanwhile at the central point of each spindle fiber appears a thickening, and these thickenings soon enlarge and unite to form a disc or plate across the cell. Along this plate a new cell-wall is laid down, which completes the division of the mother cell into two similar daughter cells. Why such a complicated process as mitosis should be necessary in cell multiplication we do not understand, but it is perhaps concerned with the need for making an exactly equal division of the chromatin material, since this part of the nucleus is known to be of great importance in directing the growth and differentiation of the organism.

Cell Enlargement.—Although two new cells have now been formed, they still occupy together a space no larger than the size of the original mother cell, so that no growth has as yet really taken place. The abundance of sugar and other dissolved foods, however, with which a growing region is always supplied, causes a high osmotic concentration in these young cells, and water is therefore vigorously drawn into them by osmosis. Since the newly-formed walls are very thin and elastic they stretch readily, and the small cells thus increase markedly in size until their permanent bulk is attained. During this rapid expansion the amount of protoplasm does not increase; and although it fills the whole of the young cell it is necessarily restricted in these larger ones to a thin sac which lines the wall. The bulk of the cell is now occupied by the *vacuole* or *sap-cavity* so characteristic of mature plant cells in general. This process of enlargement by absorption of water, following the production of new cells by

mitotic division, causes most of the obvious increase which we see in the size of plant parts.

Cell Maturation. The new tissue thus formed is very soft and weak, owing to the thin walls of its component cells, and the third stage in growth, *maturation*, is brought about by the transfer of an abundant supply of food into these newly-formed parts and the consequent construction therefrom of new living substance and of heavier walls until the cells have reached the normal, mature condition characteristic of the particular tissue of which they form a part.

Growing-points and Their Function.—Such, in brief, is the history of the production of new cells by which the growth of the plant body takes place. It is evident, however, that in mature plant tissues, where the cells are surrounded by thick and firm walls, cell division is no longer possible. Such tissues are thus really locked within their own walls and can grow no further. Organs like the leaf and flower, which rapidly attain a rather definite size beyond which growth no longer takes place, do not present this problem, for here the organ develops from a small mass of growing tissue, enlarges rapidly throughout its whole extent and reaches maturity in all its parts at once, when growth stops. In such organs as the root and stem, however, where growth continues more or less indefinitely and where the great bulk of the tissues are necessarily mature and functioning, there must obviously be some way of insuring the continued production of new cells. This is accomplished through the activity of *growing-points* or *meristems*, which are merely groups of cells remaining in an embryonic and undifferentiated condition, thin-walled and packed with protoplasm. These groups of permanently "young" cells occupy regions where growth is to take place, as at the tip of the root or stem or at the cambium. Such a growing-point may long remain dormant, but when it becomes active, cell division begins again within it. The newly formed cells which lie next to the already mature tissue now undergo enlargement and become themselves mature. This process does not affect all of the cells of the growing-point, however, for the portion away from the maturing cells still remains undifferentiated and continues to serve as a manufactory of young cells which are to be added to the tissue. The growing-point is thus a rather small and inconspicuous group of cells, not increasing in bulk itself, but carried progressively out-

ward on the crest of the tissue which it creates. The growing-point may perhaps be compared with the coral animals, which form only a very thin layer at the surface of the coral reef but by their activity build the reef farther and farther outward and are carried out upon it; or it may be compared to a brick-layer constantly adding bricks to the top of a wall and being carried himself high in air by the wall which he has made.

This method of growth at a definite point or layer, through the activity of a meristem, which is so characteristic of plant tissues and so different from that employed in the growth of animals, has certain consequences worthy of mention. It writes in the body an almost complete history of the plant's growth and development, for many of the first-formed tissues are still present (unless lost through decay), buried in the successively later accretions which have been added from time to time. A careful internal and external examination of a tree trunk, for example, enables us to tell almost exactly how tall and how thick the tree was at any year in its past history. An understanding of the location and activity of growing-points is desirable in the practice of the various methods of grafting and budding, for these are necessarily concerned with a manipulation of the meristematic regions.

There are two general types of growing points in most plants—*terminal* and *lateral*. The former, which develop at the tips of roots and stems, cause an increase in the *length* of these organs, and through their activity the stem grows tall and its roots spread farther into the soil. The latter, of which the *cambium* is the characteristic example, forms a ring or sheath of growing tissue encircling the root and stem throughout their entire extent and causing these organs to increase in *thickness*.

Terminal Growing-points.—The growing tip of a root furnishes a good example of a terminal growing-point, and a brief study of this region will perhaps enable us to understand more clearly just how such a type of meristem functions (Fig. 71). At the very tip of the root is the root cap, a body of dead cells continually renewed from the growing-point within as they are sloughed off by friction, and which protects the delicate root tip as it is forced through the soil. Just back of this is the meristem itself, a relatively small mass of tissue usually not more than two or three millimeters in length, and composed of small, thin-walled and richly protoplasmic cells. Cell division takes place in this region and here alone.

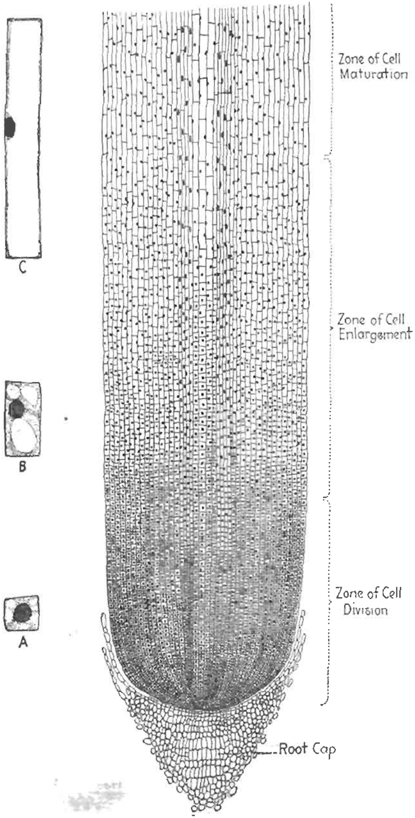

FIG. 71.—Longitudinal section of a growing root. In the zone of cell division the cells are small, rich in cytoplasm and rapidly dividing by mitosis. In the

Behind this is the zone of growth or cell enlargement, where the cells which have been formed at the growing-point stretch and elongate. It is in this zone (a few millimeters in length), and here only, that growth of the root in length takes place (Fig. 72); and it is the force exerted here by cell elongation which drives the root tip through the soil. Just back of this region, in turn, is the

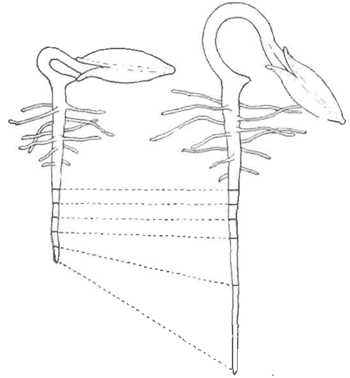

FIG. 72.—Growth of the root in length. Two squash seedlings, the one at the right a day or two older than the one at the left. The change in length of the zones between the markings, originally equidistant, shows that growth in length takes place only very near the tip of the root.

zone of maturation, where the cells, now having attained their full size, assume their mature characteristics. Here differentiation begins, the central cells developing into wood and bast, those farther out into cortex, and the outermost ones into epidermal cells and root hairs. It should be noted that the width of the young root is determined by the width of the meristem, and that no lateral growth occurs here at this time. The root grows

zone of enlargement, the cells are no longer dividing but are rapidly elongating. Vacuoles or small sap-cavities are beginning to appear in the cytoplasm. In the zone of maturation the cells have attained their final size, and the center of each is now occupied by a large sap-cavity, surrounded by a thin layer of cytoplasm. In this zone (only a part of which is shown) the cells are beginning to assume their mature characteristics and differentiation of the tissues is taking place. *A*, *B*, and *C*: cells from these three zones, much enlarged.

in thickness through the subsequent activity of a cambium farther back along the root.

The terminal growing-point at the apex of a stem resembles in its essential features that described for the root, but the zones in the growing region are not usually so clearly distinguishable and their combined length is greater. The meristem proper is at the very tip but a certain amount of cell division is going on throughout the zone of growth, which here may extend over a distance of several centimeters.

Lateral Growing-point or Cambium.—The lateral growing-point is somewhat more complicated than the terminal one and its activities are often a little hard to visualize. The best example of such a meristem is the *cambium* of the fibro-vascular cylinder of root and stem, highly developed in all typical woody plants. We have seen in our study of the stem (and except for the absence of a pith the root is essentially similar) that the fibro-vascular tissues are arranged in a cylinder, with a ring of wood inside and a ring of bast outside. Between these two rings is a very thin layer of tissue, in its resting period often only one cell in width, which is formed of the same small, thin-walled and richly protoplasmic cells which are characteristic of terminal growing-points. This is the cambium, and by its activity the fibro-vascular cylinder, and thus the whole stem, grows progressively stouter. Unlike the one-sided terminal meristems, however, this lateral growing point adds to the tissues *on both its sides* (Figs. 49 and 50). When the cambium is active and cell division is taking place, the new cells which lie on the inner edge of the cambium, next the wood, undergo a period of enlargement and maturation and become the outermost wood cells; and the new cells which lie on the outer edge of the cambium, next the bast, similarly develop into the innermost bast cells; but a zone of thin-walled "embryonic" tissue still remains between the two (Fig. 73). Thus the cambium, never growing itself, continually adds to the thickness of both its adjacent tissues. Just as the terminal meristem is carried out by the growing root or stem tip, so the cambium ring is carried farther and farther away from the center of the stem by the growing wood; and the bast, lying outside the cambium, is also carried out, not alone by this growth of the wood but by the increase in its own thickness which has taken place at its inner edge (Fig. 74). Cambial activity may perhaps be crudely pictured by comparing it to the growth of a wall

of brick (the wood) surmounted by a coping of tile (the bast); and by assuming that just at the junction between brick and tile a bricklayer (the cambium) is able repeatedly to insert a brick and a tile, the wall thus mounting upward and carrying an ever-thickening coping of tile on its top.

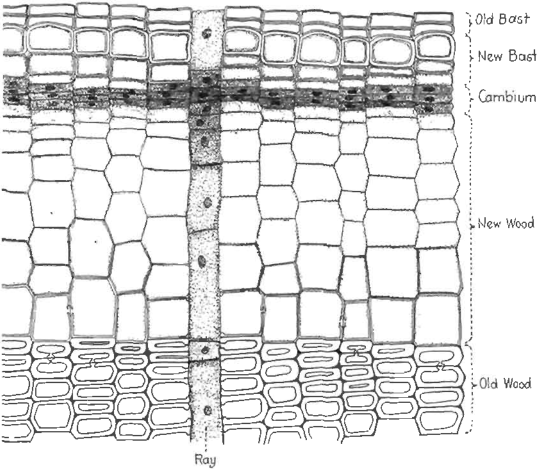

FIG. 73.—Cambium of pine stem actively producing new wood and bast. The cambium is densely filled with protoplasm. The youngest cells of wood and bast, lying next the cambium, are still small, but as they grow older they soon expand to their mature size. The new wood-cells are still very thin-walled and retain a lining of cytoplasm, which later disappears entirely.

As a consequence of this method of growth, the youngest layers of the wood are the outermost and the youngest layers of the bast are the innermost; and the past history of these two tissues, as it is preserved in their structure, should thus be read in opposite directions (Fig. 75). In woody plants, where growth in thickness is considerable and continuous, the bast, because of its rather delicate texture and the strain which is put upon it, becomes much stretched and crushed in its outer layers These are ultimately

sloughed off with the bark, whereas the wood, with its much firmer structure, remains unchanged. Well-marked growth rings are developed in the wood so that an inspection of this tissue as seen

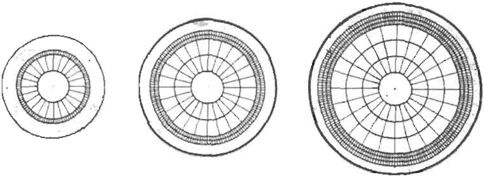

FIG. 74.—Growth of a stem in width (diagrammatic). Transverse section of three progressively older stems. Through the activity of the cambium a new layer of wood and of bast is added each year. *Pith and cortex dotted, wood plain, bast lined.*

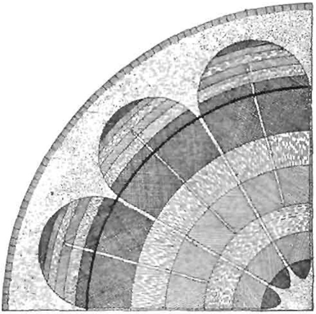

FIG. 75.—Diagram of a portion of a cross section through a six-year-old twig. The annual rings which are of the same age, in wood and bast, are shaded similarly. *(From Ganong, "Textbook of Botany", copyrighted by the Macmillan Company. Reprinted by permission.)*

in cross section makes it possible to read with much accuracy the age and past history of the plant.

Cork Cambium.—Another lateral growing-point of importance is the *cork cambium* which produces the layers of corky bark.

This may arise almost anywhere in the cortex or in the old bast, and develops on its outer face a row of corky cells which soon die and constitute the waterproof layer characteristic of bark tissue.

Primary and Secondary Tissues.—The tissues laid down by a cambium are apt to be regular in the arrangement of their cells, particularly in species where all the cells are of much the same size. This is due to the fact that each cambium cell has produced a whole row of wood cells within and of bast cells without, and that these cells are naturally arranged in a straight line along the radius of the stem passing through the cambium cell which is their common ancestor (Fig. 73).

Tissues produced by a cambium are known collectively as *secondary* tissues, and they all display in cross section this rather regular arrangement of their cells. *Primary* tissues are those which arise from a terminal growing-point, and in cross section their cells are apt to be arranged irregularly. The epidermis, cortex, and pith, and the first formed wood and bast, are all primary in their origin. The great bulk of the wood and bast in woody plants, together with the corky bark, is all secondary.

Differentiation.—Growth is not mere increase in size but gives rise to definite organs and organ systems, which are markedly different in structure and function. The factors which cause and direct this *differentiation* of the plant body as growth takes place are not understood, but we know that the process may be somewhat modified by various factors. Artificial removal of one part of the plant, such as is brought about by pruning, will stimulate the growth of the rest, and the removal of one organ or organ group will often hasten the production of more organs of this particular type. The development of certain organs is also dependent on the fulfillment of certain rather definite external or internal conditions. In most perennial plants, for example, the reproductive structures (flowers and fruit) develop only after the plant has succeeded in accumulating an ample supply of reserve food from which they may be built. Whatever stimulates very rank growth of the vegetative parts, such as an abundance of water and nitrate salts, will tend to retard the development of floral organs, and conditions of the opposite sort, (providing a sufficient supply of reserve food is at hand), will favor reproduction. The amount of photosynthetic activity, governed chiefly by the number of hours of sunlight available per day, also has an important influence on the appearance or suppression of the

reproductive structures. By skillful manipulation, the growth and differentiation of the entire plant may thus to a certain degree be brought under control.

QUESTIONS FOR THOUGHT AND DISCUSSION

441. What is the chief difference in method of growth between animals and plants?

442. With what other important difference between animals and plants is this difference in method of growth associated?

443. What disadvantage would there tend to be in very large cells? In very small ones?

444. What factors are there which tend to limit the size to which a tree can grow?

445. In what direction, or plane, with reference to the rest of the stem are most of the cell divisions which take place at the terminal growing-point of the stem? at the cambium?

446. What difference in shape would you expect to exist between the cells at a terminal growing-point and those at a cambium?

447. The zone in which elongation occurs in the root tip is much shorter than it is in the stem tip. Of what advantage is this fact to the plant?

448. Growing-points of plants are usually good to eat and in a few cases are important human foods. Why is this so?

449. The bark will separate very easily from the wood of a twig in the spring but usually at no other season. Explain.

450. If a nail is driven into a tree trunk at a point 3 feet from the ground, what position will this nail occupy in the tree 30 years later? What evidence from observation have you for your answer?

451. In just what part of the stem does growth of the pith take place? of the wood? of the cortex? of the bast? of the epidermis?

452. Is the pith in a one-year-old twig wider or narrower than it is in a 20-year-old branch grown from that twig?

453. Where would you find the cortex in a tree trunk?

454. What important changes in the size and character of its tissues take place as a one-year-old twig grows into a 20-year-old branch?

455. Why is the bark of a tree almost always rough and cracked?

456. Why does the bark of a tree never become as thick as the wood?

457. If you were to determine the age of a tree by counting the annual rings, *where in the tree would you make the count? Why?*

458. In a cut stump, the rings are usually wider next the pith than they are far out in the trunk. Why?

459. How can we use the annual rings of old tree trunks to study past climatic conditions? What cautions must we observe in doing so?

Note.—In grafting, a small twig (the *scion*) which has been cut from one plant is placed in close contact with a branch of another plant (the *stock*). This may be done in several ways, but in all cases the tissues of the stock and scion are both cut open and so placed together that the cambium of one touches the cambium of the other. If the operation is successfully performed, the stock and scion will unite and the latter will grow out as a branch of the former.

460. In the process of grafting, why is it necessary for the cambial layers of stock and scion to be in close contact?

461. After a graft has been successfully made, how does water get from the tissues of the stock into those of the scion?

462. Why is it important to use a very sharp knife in grafting operations?

463. In grafting, why is it necessary to cover the cut surfaces with wax or a similar substance?

464. Plants which are not rather closely related to one another *cannot be grafted together. What explanation can you suggest for* this fact?

465. Monocotyledonous plants can almost never be grafted. Why?

466. Nurserymen sometimes slit the bark lengthwise on strong and rapidly growing stems to hasten the production of new wood. Why does this practice aid in producing the desired result?

Note.—Pruning is the process by which certain twigs or branches are removed from cultivated trees in order to attain some desired result.

467. Why does careful pruning make a tree more vigorous and healthy?

468. Why is pruning generally done in spring, fall or winter rather than in summer?

469. How differently would you prune a tree if you desired fruit production from the way you would prune it if you desired the production of timber?

470. When a branch is cut from a tree, the wound thus caused will usually heal over. How does this healing take place?

471. If a branch is cut off very close to the trunk it will heal over much more readily than if a stump is left projecting out some distance beyond the trunk. Why?

472. Why are rapidly growing plants tenderer than slowly growing ones?

473. Why do asparagus stalks become tougher and less desirable to eat as they grow older?

474. What is the best season to train woody vines upon trellises and arbors or to fix the permanent shape of woody plants in other ways? Why?

475. *Trees in exposed places are permanently bent in the direction* of the prevailing wind. Why?

476. To develop large blossoms on a chrysanthemum plant, growers cut off all flower buds but the terminal one. Why has this the effect desired?

477. If tobacco plants are "topped," (the upper part of the stem, including the small leaves and the flower cluster being cut off when it has begun to develop) the lower leaves on the stem, which are the valuable ones commercially, will grow larger than they otherwise would. Explain.

478. Which do you think will bear fruit first, a young seedling apple tree or a scion of the same which has been grafted into a large tree? Why?

479. Why does a pruning of some of its roots often cause a tree to bear more flowers and fruit?

480. Why do many plants flower earlier if grown in pots than if grown in the open soil?

481. Why is it that apple trees, and many other northern fruit trees, sometimes grow well in warm climates but never bear much fruit there?

482. Why is a moist season good for forage crops but poor for seed crops?

483. In most plants which produce bulbs, it generally takes several years before a plant raised from seed will begin to flower. Explain.

484. Why does an apple tree usually bear a large crop only on alternate years?

485. Does it pay to take good care of an apple tree on the years in which it does not bear heavily? Explain.

486. By what methods would you encourage a plant to flower?

REFERENCE PROBLEMS

72. Are all the chromosomes in a plant cell exactly alike?

73. Give an example of a food product which is derived from a plant growing-point.

74. What are the differences between propagating plants by *cutting, budding*, and *grafting?*

75. In grafted trees, does the stock have any effect on the growth and character of the branch that develops from the scion?

76. How are "dwarf" fruit trees produced?

77. What is meant by the "polarity" of a branch?

78. At what time of the year is it determined whether a bud which is forming on an apple tree will be a leaf bud or a flower bud?

79. Give the derivation of the following terms and explain in what way each is appropriate:

Mitosis	Meristem	Chromosome

CHAPTER IX

THE PLANT AND ITS ENVIRONMENT

The form which a plant assumes and the activities which it carries on are due to the combined effect of two major causes. These are, first, the *inherent characteristics* of the plant itself, determined by the specific constitution of its protoplasm and transmitted from one generation to another by heredity; and, second, the surroundings or *environment* in which the plant lives. Plants are so diverse and environments so varied that the relations which exist between the one and the other are many and complicated. A study of these relations forms the subject matter of the science of Plant Ecology, some of the problems of which we shall discuss briefly in this chapter.

It is evident that even for the same plant, growing in the same spot, the conditions of light, temperature, moisture and various soil factors may change radically. Between two plants in different places, environmental differences may be even more marked. We have already learned enough of plant physiology to know that these various external factors may vitally affect the way in which the plant functions, and it is therefore evident that if a plant is to thrive and maintain itself, it must be able to modify its form and activities to meet this ever-changing environment successfully. One of the most remarkable facts of biology is that organisms do possess, in greater or less degree, this characteristic of advantageous *regulation* of structure and function in conformity to the changing external world. As to what are the causes of these regulations there is much difference of opinion and no certain knowledge. In describing plant activities, most of which contribute so obviously to the welfare of the individual, we continually find ourselves using terms which imply *purpose* or *effort*. It is indeed very difficult to describe the facts of form and function in simple language without tacitly assuming that there is within the plant something which directs and regulates its life so that it will tend to do whatever is to its own best advantage. Such an assumption is, of course, quite contrary to the modern

scientific attitude as to plant physiology, which demands for every observed change a definite physical cause and not a psychological one; and it introduces a deeper problem which is clearly the province of the philosopher rather than of the botanist. The latter should content himself with carefully recording all changes induced in the plant by a changing environment, and with analyzing as carefully as possible the factors which seem to be responsible for these changes.

Stimulus and Response.—In such a study it is important to remember that the environmental forces do not act on the plant as they would on a lifeless body—on a stone or a drop of water, for instance—merely raising its temperature, illuminating its surface, pulling it down by gravity or affecting it in other direct ways; but, *instead*, that each of these forces acts as a *stimulus* which brings forth on the part of the plant a definite *response*. This response may be either a change of function or a change of structure. To the same stimulus the response of one plant may be very different from that of another, and the responses of different parts of the same plant may also differ greatly. The stimulus is merely a trigger which releases a response. Just what a given response shall be depends entirely upon the constitution of the living substance of the plant itself. This characteristic trait of protoplasm whereby it is continually reacting or responding to stimuli is known as *irritability* and is a distinctive quality of all living things. In animals, protoplasmic irritability is extraordinarily developed in nervous tissue, which receives the stimuli and controls the responses of the organism. In plants, however, no nervous system has been differentiated, and although some regions are much more sensitive than others and may evidently transmit the effects of a stimulus for a considerable distance, it is the protoplasm of the ordinary cells which is chiefly concerned in the many responses made by the plant.

It should be noted that although mature parts of the plant, particularly those which are soft in texture, are able to change their form and position to some extent through regulating the turgidity of their cells, it is the young and growing regions which are most sensitive to stimuli and are thus best able to bring about regulatory changes of structure and position.

In any discussion of the effect of the environment we should consider not only the reaction of the individual plant but should also look at the problem from the historical viewpoint and study

those inherited characteristics which enable it to thrive in a particular environment and which have become implanted in the species during the course of its evolution. Adjustments of this kind, either of structure or function, we usually speak of as *adaptations*. The natural adaptations of cacti for desert life and of orchids for insect fertilization may be cited as examples.

We have called attention to the complexity of the environment in which the plant grows. The first step in an analysis of the

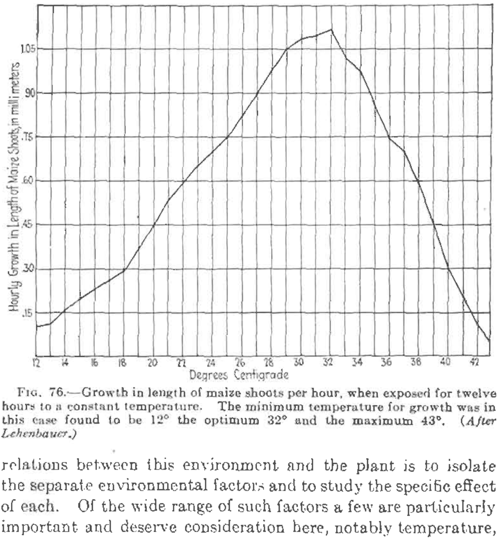

FIG. 76.—Growth in length of maize shoots per hour, when exposed for twelve hours to a constant temperature. The minimum temperature for growth was in this case found to be 12° the optimum 32° and the maximum 43°. (*After Lehenbauer.*)

relations between this environment and the plant is to isolate the separate environmental factors and to study the specific effect of each. Of the wide range of such factors a few are particularly important and deserve consideration here, notably temperature, light, gravity, moisture, and various chemical substances, which constitute the *inorganic environment*; and the *surrounding plants* and animals, or the organic environment.

Temperature.—It is characteristic of all vital processes that their maintenance is possible only within a comparatively narrow range of temperatures, and temperature changes therefore elicit

marked responses in the activity of protoplasm. In general, active life is possible for the higher plants between 0 and 50° Centigrade, although these limits vary much from one species to another. The lowest temperature at which a given plant can continue to live is known as its *minimum* temperature and the highest as its *maximum*. At some point between these two the plant displays its greatest activity and this point is known as its *optimum* temperature (Fig. 76).* The various physiological processes which go on within the plant, such as photosynthesis, respiration, and growth, each have their minimum, optimum, and maximum temperatures and these are not necessarily the same for the different processes.

Members of the vegetable kingdom lack the high and delicately maintained body temperature which is characteristic of the higher animals, and the temperature of most plants follows rather closely that of their environment, absorbing heat or losing heat as the environment becomes warmer or colder. About 25 per cent of the radiant energy from direct sunlight, and a much larger percentage in diffuse light, is absorbed by the plant. Most of this is converted into heat, only a small fraction of the energy being used in photosynthesis. This heat would often raise the temperature of the plant above the maximum if it were not largely expended in evaporating water from the plant tissues, and the importance of transpiration as a cooling process is thus again to be emphasized. The body temperature of the plant may sometimes fall a little below that of its immediate environment, owing to excessive radiation or evaporation; or it may sometimes rise noticeably above it owing to the release of heat during respiration, especially in regions where growth is active. The latter phenomenon is particularly conspicuous in the case of intense bacterial action, for the amount of heat liberated by the vigorous respiration of these lowly plants is often sufficient to raise the surrounding temperature markedly.

The problem of the temperature relations of plants is further complicated by the fact that a plant may often become accommodated or "acclimatized" to temperatures higher or lower than the usual limits for the species, if the plant is brought into the new environment very gradually. Thus plants which would normally suffer from cold at a given temperature may often be made to

* These terms *maximum*, *minimum* and *optimum* are also used for other environmental factors, notably light and moisture.

thrive under it by lowering the temperature gradually. This resistance of plant tissues to heat and cold is also dependent to some degree on maturity, for young and growing tissues are much more susceptible to injury therefrom than older ones. In general, within any particular species, the ability to withstand high and low temperatures is correlated with the amount of water in the cells and particularly in the protoplasm itself. Where water is abundant, resistance is low; where it is scarce, resistance is higher.

There are well-marked inherited differences in the temperature relations of plants. The optimum for an alpine plant must obviously be far lower than for a native of the tropics. Certain algae have their normal habitat in the water of thermal springs and others in the frigid arctic seas. Melons have a much higher optimum than peas, and some varieties of apple, peach, and plum are distinctly "hardier" than other varieties.

Light.—We have already noted the essential part which light plays in the life of green plants through its influence upon the process of photosynthesis. From light rather than from heat, electricity or other sources, the plant derives the kinetic energy which it stores up in potential form in its food; and in this important capacity of an energy-provider light is therefore essential to all plants. This influence is evidently an indirect one, however, particularly in the case of non-green plants, for most of these thrive in the absence of light as long as their food supply holds out.

Quite apart from its indirect role in nutrition, light exerts certain direct effects. Most notable of these are the growth *movements made by plant parts in response to the stimulus of illumination.* Not all plants and not all parts of plants respond in the same way to this stimulus. As a general rule the stem will turn toward the source of light, the root away from it, and the leaf, by the twisting of its petiole, will assume a position in which the broad surface of the blade is at right angles to the light rays (Fig. 77). Any movement which is a specific reaction to the stimulus of light is known as a *phototropism.* A normal stem is therefore said to be *positively phototropic,* a root *negatively phototropic,* and a leaf *neutrally phototropic* or *diaphototropic.* Although the results of phototropism are usually much more noticeable where a plant receives its illumination from one side only, it plays an important part in the orientation of plant

structures generally. The advantageous character of the ordinary phototropic responses is obvious.

Not only does light affect the position of plant organs but it has a profound influence upon their structure. The stems of green plants grown in the dark are usually slender, much elongated and provided with but little woody tissue; and their leaves are

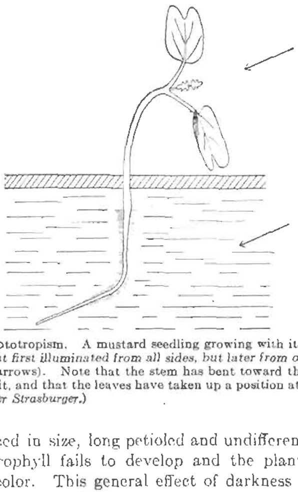

FIG. 77.—Phototropism. A mustard seedling growing with its root in water. *This plant was at first illuminated from all sides, but later from only one (shown* by direction of arrows). Note that the stem has bent toward the light and the root away from it, and that the leaves have taken up a position at right angles to the light (*After Strasburger.*)

greatly reduced in size, long petioled and undifferentiated internally. Chlorophyll fails to develop and the plant assumes a pale yellow color. This general effect of darkness is known as *etiolation* (Fig. 78) and begins to show itself whenever the supply of light falls below the optimum either in duration or intensity. If sufficiently pronounced, etiolation ultimately results in death. The stimulus of light upon protoplasm evidently prevents the abnormal growth which we see in etiolation, but how this effect is brought about, we do not understand.

Too little illumination is thus harmful to the plant, but too much may be equally so through its toxic effect upon protoplasm. To the blue, violet, and ultra-violet rays living substance is particularly sensitive, and in many plants the position or

structure of parts may be so modified that as small a surface as possible is exposed to light when it becomes very bright. In some

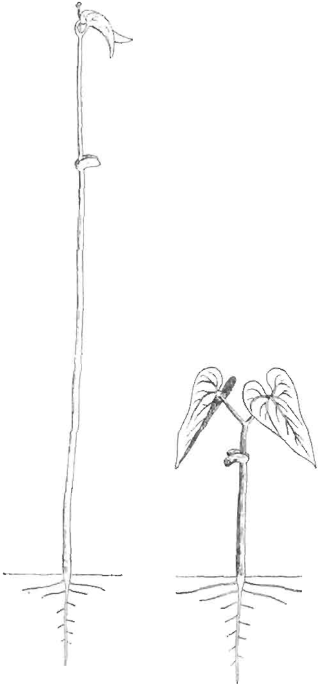

FIG. 78.—Etiolation. The two bean seedlings are of the same age but the one at the right was grown under normal illumination, the one at the left, in darkness. Note the longer internodes, the paler color, and the poorer leaf-development of the darkened plant.

species, for example, the broad surface of the blade is exposed to light of moderate intensity but only the edge to very bright illumination.

Toward light, as toward temperature, plants display certain inherited adaptations. Some green plants are able to thrive in light of comparatively low intensity and are said to be *tolerant* (Fig. 79), in the sense that they will tolerate a considerable degree of shade. Others will grow normally only where the illumination

FIG. 79.—Plants tolerant of shade. These broad-leaved plants of *Viburnum* are able to thrive on the forest floor, where the lower branches of the forest trees have died from lack of light.

is good, and are said to be *intolerant* (of shade). Some are sensitive to intense light and thus cannot live in the open, whereas others, either through the greater resisting power of their protoplasm or through various structural modifications, are able to withstand the most brilliant sunlight.

Gravity.—Gravity in its effect upon plants is unlike temperature and light in that it is both continuous in action and constant in amount. *It is a very important factor in determining the direction of growth in plant parts and, like light, it affects different organs in different ways.* Any reaction to the stimulus

of gravity is known as a *geotropism* (Fig. 80). Stems ordinarily tend to grow in a direction opposite to the force of gravity and are thus *negatively geotropic.* Primary roots and certain other portions of the root system, on the contrary, tend to grow directly toward the center of the earth and are thus *positively geotropic.*

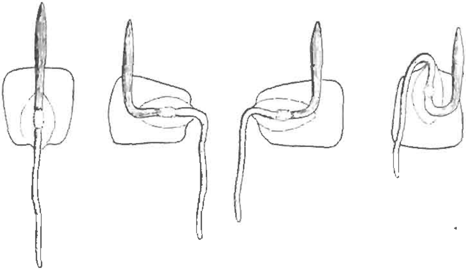

FIG. 80.—Geotropism. Four kernels of corn which have germinated in different positions. The young root in every case has grown downward and the young shoot upward.

Most leaves tend to take up their position at right angles to the force of gravity and many lateral roots also grow in an approximately horizontal direction. Such organs are said to be *diageotropic.* The advantage of these specific tropisms to the plant is obvious.

Plants differ considerably in their inherited adaptations to the influence of gravity. Stems of prostrate plants have lost their negative geotropism and may even develop into rootstocks or tubers which react toward gravity like roots. The responses of flowers and fruits to this stimulus are also very diverse and for the most part seem to be advantageous to the plant.

The mechanism of stimulus and response has been more carefully studied in the case of geotropism than with other environmental factors. If very young seedlings in which the root and stem are just appearing are fixed in any position whatever, the young root will invariably grow downward and the young stem upward (Fig. 80). By attaching such seedlings to a disc and revolving it rapidly, centrifugal force may be developed which is greater than gravity, and in such a case the young plants orient

themselves to this new stimulus, the roots growing outward in the direction of the force and the stems inward, in the opposite direction. The force of gravity may also be practically eliminated, without such a substitution of another and more powerful force, if the disc to which the seedlings are attached is slowly revolved in a vertical plane by clockwork, thus exposing all sides of the seedling successively to the stimulus. Under these conditions, the root and the stem continue to grow in the direction in which they happened to start with no reference at all to gravitation. The pull of gravity, or any other force which we may substitute for it, must therefore be able in some way to stimulate the growing regions of root and stem so that growth occurs in certain definite directions. It has been proven that the very tip of the root, for a distance of approximately 1 or 2 millimeters in length, is the only portion which is sensitive to the stimulus. If this region is pointing downward, no bending of the root will take place, regardless of the position of the rest of the organ. If this region is horizontal, however, the root will bend downward until the sensitive tip itself points downward again. The actual bending never takes place in the tip, however, but always in the growth zone some distance behind. As to how the stimulus is perceived by the tip, and how it is transmitted to the zone of bending, are problems about which little is definitely known.

Moisture.—Of vital importance to every plant is the maintenance within it of a sufficient supply of water, and we have already called attention to the preponderant role which this substance plays in plant functions. It comprises over ninety per cent of most living plant tissues. Practically all of the physiological processes of the plant are carried on in solution within it. The transportation of substances from place to place through the plant body is accomplished by their diffusion (in solution) from one cell to another. Water is one of the two essential raw materials in photosynthesis. The normal form and proper functioning of the softer plant tissues is maintained by keeping their cells completely filled and turgid with water. It is therefore to be expected that the characteristic structures and activities of plants should be concerned with obtaining and conserving an ample supply of this precious liquid.

Definite movements and changes of position with reference to moisture are shown chiefly by roots. The root tip is sensitive to variations in the water-content of the soil, and will turn from a

region of low content to one of higher. Such a response is known as an *hydrotropism* and results in the pursuit of moisture by roots for considerable distances, notably when the surface layers of the soil are drying out and the water table is descending.

It is in responses of structural change rather than those of movement, however, that the effect of moisture is most often manifest. Plants which have access to abundant water supply

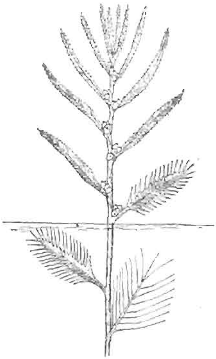

FIG. 81.—"Amphibious" plant. A shoot of mermaid weed (*Proserpinaca palustris*). Submersed leaves are finely divided, aerial leaves undivided, and leaves between, intermediate in form.

grow luxuriantly, for the most part, with large leaves and rather soft tissues. Cuticle and epidermis are thin, woody tissues somewhat weak, and parenchyma abundant. A similar plant grown where water is scanty becomes stunted throughout and has much smaller leaves. Its tissues, particularly the epidermis and cuticle, are much tougher, and the woody elements stronger and more abundant. In some instances even more profound structural changes are produced. The water buttercup, to cite a notable example, when growing on the shore produces normal buttercup leaves, but when submersed in water develops leaves which are dissected into fine capillary segments and are thus particularly well fitted for aquatic life. Other "amphibious" plants exhibit similar structural changes (Fig. 81).

Xerophytes.—Inherited adaptations to abundance or dearth of water show the pronounced effects of moisture as an environmental factor. Many plants have become so modified during the course of evolution that they are able to thrive under conditions where the available soil water is comparatively small in

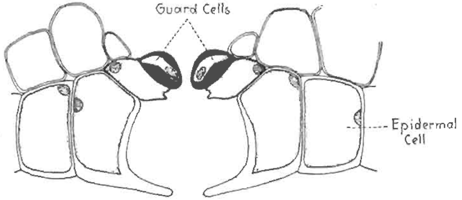

FIG. 82.—The stoma of a xerophytic plant (*Cycas*). The stoma is protected by being sunken in a pit formed by the over-arching growth of two adjacent epidermal cells.

amount, and where plants without special adaptive modifications would speedily perish. Such drought-loving plants are known as *xerophytes* and are characterized by several types of structural and functional modifications which result in a notable ability

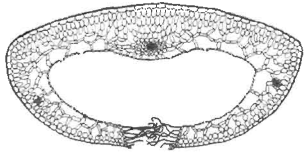

FIG. 83.—Section across the blade of a xerophytic leaf (*Empetrum*). The blade is rolled back so that the margins almost meet, thus preventing excessive transpiration from the stomata, which are on the lower (inner) surface. A felt of woolly hairs is also developed at the leaf margins which further hinders the loss of water.

both to draw water from the soil and to retain it in the plant tissues. The root-system is very well developed in proportion to the shoot. The osmotic concentration of the cell sap is usually higher than among plants growing under less arid environments. The leaf surface is reduced, sometimes very radically; and leaves may even disappear entirely. The cuticle of stem and leaf

FIG. 84.—One type of xerophyte. The stonecrop (*Sedum*), showing its ver thick and fleshy leaves.

FIG. 85.—Hydrophytes. The type with broad, floating leaves (water lily) and that with small, delicate leaves, mostly submersed (water milfoil), are both shown.

becomes extraordinarily thick. Stomata are relatively few and are usually either sunken in pits (Fig. 82), covered with a mass of hairs, or otherwise protected (Fig. 83). In certain cases, notably among arctic and alpine xerophytes, the leaves and stems are covered with a felting of hairs. In others, particularly the xerophytes of saline soils, the vegetative organs become fleshy and succulent (Fig. 84). Internally, most xerophytes have an abundant development of woody tissue.

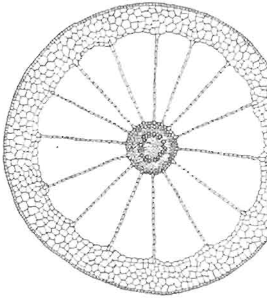

FIG. 86.—Transverse section of the stem of a typical water-plant (*Myriophyllum*). The fibro-vascular cylinder is poorly developed and the cortex is provided with large air chambers.

Hydrophytes.—At quite the opposite extreme from xerophytes are those plants which are adapted to live nearly or quite submersed in water. These *hydrophytes* (Fig. 85) have root-systems which are much reduced or may even be entirely absent. The leaves, if submersed, are usually finely cut and dissected and are very thin. Stomata are absent. The stems have become very soft and weak and possess an exceedingly small amount of woody tissue. In certain types, notably those in which the leaves (or some of them) are exposed to the air, the tissues of the plant are well provided with air passages (Fig. 86).

Mesophytes.—Those plants with which we are most familiar thrive best on a moderate supply of water and are known as *mesophytes*. Living under conditions especially favorable for plant growth, they possess well developed root and leaf systems and are generally large, thrifty, and fast-growing as compared

with xerophytes and hydrophytes. Their leaf area is extensive, the cuticle and epidermis rather thin, and the stomata not especially protected. *Internally they are highly differentiated, particularly as to the fibro-vascular system.*

Through bog and swamp plants, with their typically spongy internal structure, mesophytes merge gradually into hydrophytes; and at the other environmental extreme it is hard to draw a sharp line between mesophytes and xerophytes. Furthermore, there are many plants, such as our deciduous trees, which are mesophytic during the summer and xerophytic during the winter. Such plants are known as *trophophytes*.

The modifications of plants with reference to their water supply are legion and provide a fascinating field of investigation, for nowhere else is the regulatory character of plant structures more clearly evident.

Chemical Substances.—The effects of chemical substances upon plants are many and far-reaching. In certain cases, particularly in the lower groups, the direction of growth or movement may be determined by chemical stimuli. Far more profound are the structural and functional changes induced by chemical substances entering the plant from the soil.

We have already enumerated the chemical elements which are essential to the life of plants and have called attention to certain of their specific effects. Iron, for example, has been found to be necessary for the production of chlorophyll. Phosphorus is abundant in seeds and is believed to stimulate the development of reproductive structures. Potassium seems to have an intimate relation to the process of photosynthesis and an ample supply of this element is necessary if the leaves are to become well developed and to function vigorously. Nitrogen, especially when accompanied by an abundant water supply and active photosynthesis, markedly stimulates the development of vegetative organs and tends to delay the production of flowers and fruit. These elements and others not only affect the vigor and size of the plant but often the shape and structure of its parts.

Chemical substances injected into the plant body are also able to stimulate growth in various abnormal ways. Notable instances of this are the great variety of galls produced on plant tissues through insect stings or fungus attacks (Fig. 87).

Plants display characteristic inherited reactions to the presence of chemical substances in the soil. Certain species, for example,

thrive on saline soil where the majority of plants are quite unable to exist. Others grow only where the soil is markedly acid, and still others only where lime is abundant. Some ubiquitous types are able to exist in soils of almost any chemical composition. The distribution of plant species over the earth's surface is influenced to no small degree by their reactions to particular chemical substances in their environment.

A number of species may be all adapted in a similar way to these various physical conditions of the environment which we

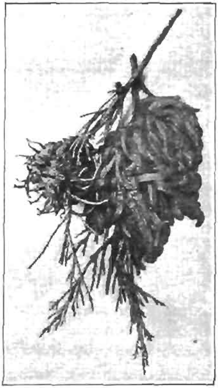

FIG. 87.—Galls produced by the attack of a fungus (*Gymnosporangium*) on red cedar.

have just been discussing and may thus grow side by side together, forming an easily recognizable group. Such a group is known as a Plant Association. We may distinguish, for example, a Swamp Association (Fig. 88), a Desert Association (Fig. 89), a Mesophytic Forest Association, a Sea Beach Association, and many others, each with its characteristic species and its characteristic structural and functional modifications. As the environment changes, one association may encroach upon another and the vegetation of a region may thus be gradually altered. A study of plant associations and their history is an important part of the science of ecology.

FIG. 88.—A Swamp Association. Note the contrast between the plants which compose this Plant Association and those in Fig. 89.

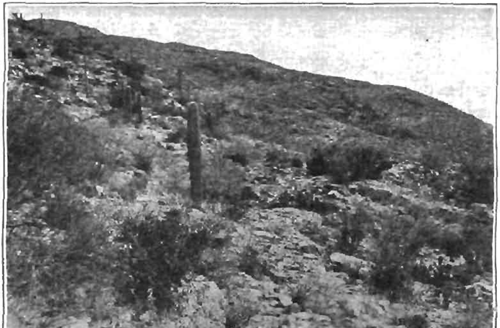

FIG. 89.—A Desert Association, composed of cacti and other extreme xerophytes. (*Courtesy of D. T. MacDougal and Forrest Shreve, Desert Laboratory, Carnegie Institution.*)

Living Organisms.—The environmental factors which we have been discussing thus far are all lifeless ones. Of the utmost significance to the plant are also the living organisms with which it is surrounded. Its relations to this organic environment are many and varied. First in importance is the struggle for

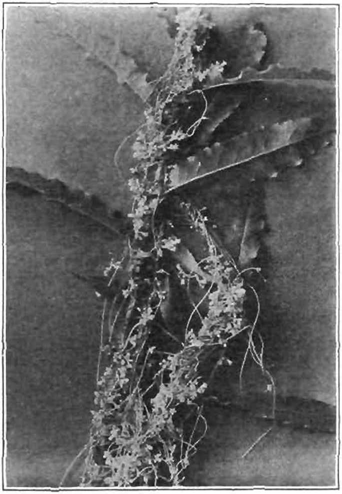

FIG. 90.—A parasite. The dodder (*Cuscuta*) parasitic on an herbaceous plant. Note the absence of chlorophyll and the reduction of leaves to scales.

survival which is taking place continually between living things. No plant exists by itself, reacting only to the inorganic factors which surround it. It is competing with its neighbors for water, for nutrient materials, for sunlight, for insect visitors, and for other necessities. It is preyed upon by parasitic plants. It is devoured or destroyed by animals of all kinds. Only the vigorous and the fortunate succeed, and they are few compared with the hosts which fail and die.

Parasites.—The great majority of the seed plants are independent, deriving their sustenance directly from the inorganic environment, and the struggle between them is therefore fair combat, with victory to the most efficient. Some species, however, have abandoned this passive form of competition for active attack upon their neighbors and have developed an ability

FIG. 91.—A parasite. The American mistletoe (*Phoradendron*), parasitic on a tree.

to obtain part or all of their food directly from the tissues of other plants. Such an organism is known as a *parasite* (Figs. 90 and 91) and its victim as its *host*. The tissues of the host plant are pierced by small, modified roots, the sucking organs or *haustoria*, which may be developed either from the root or the stem of the parasite. These penetrate to the vascular bundles or storage regions of the host and draw therefrom a supply of manufactured food. Parasites display certain characteristic structural modifications, notably an absence or poor development

of normal roots, a reduction in size of the leaves, and a partial or complete loss of chlorophyll. Some parasites, particularly those whose roots attack the roots of other plants, may be only *partially parasitic*, whereas others derive their entire food supply from their hosts and can live only as parasites.

The small but interesting group of insectivorous plants have gone a step further and reversed the ordinary relation between animals and plants by becoming parasites upon insects. These plants capture their prey either by a closing trap, as in the

Fig. 92.—An insectivorous plant, the sundew (*Drosera*). In the sticky tentacles of its leaves, insects become entangled.

Venus's Fly Trap; a pouch of liquid, as in the Pitcher Plants, or a mass of sticky tentacles, as in the Sundews (Fig. 92). Once caught, the bodies of the insects are apparently digested by enzymes secreted by the plant, and may thus furnish a small supply of nitrogenous food. Parasitism is comparatively rare among seed plants but is very common in the fungi, many of which attack the tissues of both plant and animal hosts, producing serious bacterial and fungous diseases.

Saprophytes.—Similar in certain respects to parasites are a group of plants which also depend upon other organisms for food instead of manufacturing it independently from raw materials. This group, however, does not attack living animals and plants but lives instead upon their dead bodies, drawing therefrom the already combined organic compounds and using them directly as food. Such plants are known as *saprophytes*. Here belong the bacteria of decay and all bacteria and other fungi which are not parasites. There are a few saprophytes among seed plants, of which the Indian Pipe (Fig. 93) is perhaps the

best-known example. The structural modifications of such forms are in general similar to those which distinguish parasites. The ability possessed by both parasites and saprophytes to use complex organic substances directly is nearly or quite lacking among ordinary green plants, which are able to take through their roots only simple inorganic salts.

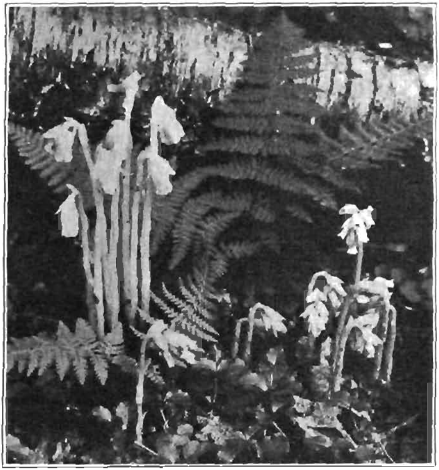

FIG. 93.—Saprophytes. The Indian Pipe (*Monotropa*).

Epiphytes.—A third type of relationship between one plant and another, and one which is free from destructive consequences, is presented by those species which grow upon the bodies of other plants but are not parasitic thereon. Such plants are known as *epiphytes* (Fig. 94) and are especially common in dense tropical forests. Many ferns and orchids display this habit of growth. The roots of epiphytes have no connection with the ground and do not enter the living tissues of other plants, and in consequence they are often modified to draw moisture directly

from the rain and dew. Structural features characteristic of these plants are a much thickened cuticle, protected stomata, and fleshy stems and leaves.

Symbiosis.—In the relationships between the plant and other organisms in its environment which we have mentioned, the advantage has been one-sided. There are instances, however, of true *symbiosis*, an intimate relation between two plants, or

FIG. 94.—Epiphytes growing on a tree-trunk.

between a plant and an animal, where the advantage, to some extent at least, is mutual. A notable example of this is provided by the whole group of Lichens, each member of which is a composite organism produced by the close association of a species of alga and a species of fungus (Fig. 182) and in which both seem to derive a certain amount of benefit from the union. The mycorrhiza, or association between a fungus and the root tip of a higher plant, which we have mentioned in a previous chapter, is evidently another example of the same state, as is probably the connection between the nitrogen-fixing root-tubercle bacteria and the leguminous plants in which they live.

Passing higher in the vegetable kingdom, we find many instances of relationship between organisms which are also apparently

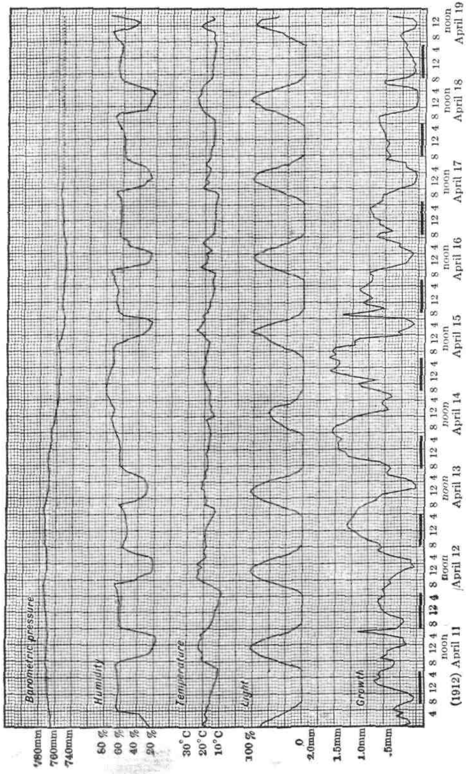

FIG. 95.—Graph showing the hourly rate of growth of a flower-stalk of grape hyacinth, and its relation to several important factors in the environment. (*From Ganong, "The Living Plant", Henry Holt and Co.*)

of advantage to both though they are not intimate enough to class as true symbioses. Most notable are those between flowering plants and insects, whereby the plant derives the benefit of cross-pollination and the insect a supply of nectar; and the numerous cases where fruits are attractive to animals by furnishing them with food, and are in turn distributed widely by these animals, with consequent benefit to the plant species. These two types of relationship are very numerous and fascinating and have long been the subject of investigation by botanists. We shall describe them more fully in a later chapter.

In this brief discussion of the influence upon plants of the various factors in their environment, we have merely outlined some of the important aspects of the problem which underlies the whole science of ecology. No one of these factors is paramount, and the reaction of the plant is to the whole series of them (Fig. 95). The direction of growth, for example, may be influenced both by gravity and by light, and the result is determined by *the relative strength of these two stimuli under the particular conditions existing in a given case.* In the same way, the distribution of a given plant species over the earth's surface is determined not alone by soil conditions or moisture or temperature or parasites, but by the whole series of environmental factors taken together. The *essential point to remember* is that the structure and activities of any plant are not entirely controlled either by the environment in which it lives or by the specific and inborn characteristics of its protoplasm, but are results of an interaction between these two forces. Plants *belonging to different species will develop and function very* differently even under environments which are identical; and plants entirely similar will become very different if grown under different environments. We are here facing the ancient problem of Heredity *versus* Environment, which confronts man in so many fields of inquiry.

QUESTIONS FOR THOUGHT AND DISCUSSION

487. Give an example of the response of a plant to its environment which is regulatory in character.

488. What do we mean by saying the "no nervous system has been differentiated" in plants?

489. From its structure, which of the tissues of the plant do you think might serve most readily as a means of transmitting stimuli quickly from one part of the plant to another, in somewhat the same way as do the nerves among animals?

490. Is there anything in the plant corresponding at all to the sense organs of an animal?

491. Give an example of an adaptation of a plant species to the environment in which it lives.

492. What danger may there be for a plant species in becoming very closely adapted to a particular environment?

493. Why are plants more susceptible to frost when water is abundant in their tissues than when it is not?

494. Rank, rapidly growing parts of plants are apt to be injured first by frost. Why?

495. Why is a slight frost in fall or spring often more disastrous to plants than very much lower temperatures in the middle of the winter?

496. Why will a warm period in midwinter often prevent a fruit tree from bearing fruit the next season?

497. It is better not to fertilize trees or shrubbery heavily in the late summer and fall. Why?

498. A frost while fruit trees are just in bloom is more harmful than it would be a little earlier or a little later. Why?

499. Why do the first frosts of autumn usually come in low land?

500. Why will an orchard of such fruit trees as the peach, which are rather susceptible to cold, survive better if grown on a hilltop or on the north slope of a hill?

501. Which do you think will withstand frosts better, plants of salt marshes or of ordinary soil? Why?

502. Of what advantage and of what disadvantage is snow to vegetation?

503. Many of the higher animals can thrive and function normally in the winter whereas the higher plants cannot. To what physiological difference between the two groups is this due?

504. Of what advantage is it to the plant to have its stems positively phototropic and its roots negatively so?

505. Since most stems are positively phototropic, why is it that all the trees in the northern hemisphere are not bent somewhat toward the south?

506. Flowers are generally positively phototropic and fruits negatively so. Of what advantage are these reactions to the plant?

507. When nurserymen grow seedlings of forest trees, they cover the plants with a lattice-work screen for the first few years. Why?

508. Most plants in darkness grow abnormally long. Of what advantage may this reaction be to the plant?

509. Of what advantage is it to the plant for its roots to be positively geotropic and its stems negatively so?

510. Give an example of a stem which is not negatively geotropic.

511. Give an example of a root which is not positively geotropic.

512. How different is the direction in which the trunk of a tree will point if it is growing on a steep hillside from that in which it will point if it is growing on level ground? Explain.

513. Just how differently does the force of gravity act when it causes a root to grow downward and when it causes a horizontally placed piece of wood, or other dead object, to bend downward?

514. Of what advantage to the plant is it to have its roots positively hydrotropic?

515. Why do desert plants usually have a rather high osmotic concentration in their cell-sap?

516. Crocus, narcissus, and tulip plants flower and flourish in early spring and by late spring have withered down, not to appear above ground till the following year. For what sort of a climate do you think such plants are well adapted?

517. Why are arctic and alpine plants xerophytic?

518. The leaves of many evergreens, such as juniper, are pressed against the stem in winter and loosely spread in summer. Explain.

519. The timberline (or line above which trees do not grow on a mountain side) is generally higher on a mountain range than on an isolated peak, and in ravines than on ridges. Why?

520. The "rosette" habit of growth, where all the leaves are in a circle next to the ground and a stem is absent, is common in cold, arid regions. Explain.

521. Why are mesophytes "generally large, thrifty and fast-growing as compared with xerophytes and hydrophytes"?

522. Which will produce a better crop of fruit, a warm, dry summer or a cool, moist one? Why?

523. Why should nitrates and potash be applied in large amounts only early in the growth of such a crop as beans or corn, and withheld during later growth?

524. What different treatment, as to soil richness and moisture, should you give to such crops as celery and lettuce from that which you give to beans and corn? Why?

525. Why is a Plant Association often a very heterogeneous group, consisting of trees, herbs, saprophytes, climbers and many other types?

526. What are the advantages and the disadvantages of a parasitic habit of life to a plant?

527. In the case of a parasitic plant, how are the haustoria able to penetrate the body of the host?

528. What do you think are the means by which the parasite withdraws food and water from its host plant?

529. Which type of plant do you think appeared first in evolution, the saprophyte or the parasite? Why?

530. What important roles do saprophytes play in the economy of nature?

531. Why are epiphytes more common in dense tropical forests than anywhere else?

532. Of what value to a pine tree is its pitch?

533. Of what advantage to a plant may be poisonous substances occurring in its leaves or seeds?

534. Give at least three reasons why plants which are crowded together do not grow as well as those which have plenty of room.

535. What barriers hinder the dispersal of marine plants?

536. What various reasons can you think of to explain the fact that some plant species are much more widely dispersed than others?

537. There are many more species of plants in the tropics than there are in temperate regions. Explain.

REFERENCE PROBLEMS

80. The mean annual temperatures ("average" temperature) of England and of New England are not very different Many delicate plants will grow in the former region but not in the latter. How do you account for this?

81. Compare the United States and the British Isles as to rainfall and temperature during the growing season. How do these figures explain the fact that grass grows so much better there than here, and corn so much better here than there?

82. What is meant, in ecology, by a *succession* of plant associations and what causes such a succession?

83. Although a much wider range of plants can be grown in northern Europe than in the northern United States, the latter region has far more native species than the former. Explain.

84. As a general rule, which can be used in agriculture over a wider area a breed of livestock or a variety of cultivated plants? Why?

85. Give the derivation of the following terms and explain in what way each is appropriate:

Phototropism	Etiolation	Parasite
Geotropism	Xerophyte	Saprophyte
Hydrotropism	Hydrophyte	Epiphyte
Chemotropism	Mesophyte	Symbiosis

CHAPTER X

REPRODUCTION

Thus far we have studied the plant body as an *individual*, in which roots, stems, and leaves develop characteristically and function in such a way that the successful existence of the plant is assured. The individual ultimately disappears, however, and *it is obviously necessary that if the species to which it belongs is to survive and maintain itself, some means must be provided for insuring a constant succession of new individuals by transmitting the life of one generation to another.* This is accomplished by the process which we know as *reproduction*, whereby the plant, by one means or another, produces a group of offspring. The structures and functions of all plants may thus be divided into two rather sharply marked groups: The *vegetative*, centering around the root, stem, and leaf, which are concerned primarily with the life of the individual plant; and the *reproductive*, centering around the flower and fruit, which are concerned primarily with the maintenance of the species. It is the latter group which we shall now discuss.

There are two main types of reproduction, markedly different from one another. These are *asexual* or *vegetative* reproduction, in which portions of the body of the parent become detached from it and are set apart as new individuals; and *sexual* reproduction, where there is a union between two specialized reproductive cells, from which union a new individual arises.

Asexual Reproduction.—The simplest type of asexual reproduction *consists in the division of the parent plant into two or more parts, each of which becomes independent.* It is a characteristic property of most plants that a small portion of the body, (particularly if it includes a bud) when removed and placed under favorable conditions, will replace the missing parts and develop into a new individual. This readiness for multiplication is made use of extensively in the various arts of plant propagation, by which new individuals are produced through *cuttings* and like processes. In a somewhat similar manner, a bud or twig from

one plant may be united so intimately to another by *budding* or *grafting* that it thrives and grows as an integral part of the plant to which it has been transferred. By use of these methods of artificial reproduction the horticulturalist succeeds in producing enormous numbers of individuals from a single plant. One particular advantage of such a procedure is that it insures a high degree of uniformity among the offspring, since each one of

FIG. 96.—Asexual reproduction in the strawberry. Creeping stem (runner or stolon, s) from the end of which a new strawberry plant is growing. Sexual reproduction, by flowers and fruit, is also shown on the same plant.

them is in fact a portion of the original individual. All true Concord grape vines or Baldwin apple trees, for example, are simply detached parts of the original vine or tree in which the variety originated.

In many plants, reproduction of this sort is a constant accompaniment of the slow spread and dispersal of the vegetative parts which is continually taking place (Fig. 96). Thus a grass plant may become established in one spot and gradually extend its area until it forms a considerable patch of turf. Portions of this, through accident or decay, become separated from one

another, and a colony of plants takes the place of a single individual. In a somewhat similar fashion the beech tree multiplies itself, buds arising on the roots of the parent tree until it is surrounded by a grove of beeches. This method of reproduction, however, is not very common among the seed plants.

In many species structures have arisen which are particularly adapted for aiding vegetative dispersal of the plant body and which thus partake somewhat of the nature of reproductive structures. To this group belong the *runner* or *stolon* of plants like the strawberry, the rapidly spreading rootstocks of the quack grass, and the long, arching stems of the raspberry, in which the *tips touch the ground and there take root.* Other vegetative parts are sometimes modified still further as reproductive organs. Perhaps the best known example of such is the *tuber* (Fig. 46) of the potato, which is merely a short and very much thickened underground stem, from the buds of which new potato plants arise the next season. The *bulb* (Fig. 47), as in the onion and hyacinth, and the *corm* (Fig. 47), as in the crocus, are also short, stout stems with their lower leaves modified as scales. They carry the plant over from one season to the next and their buds ultimately give rise to a group of new plants.

Sexual Reproduction.—Far commoner and more important *than the asexual or vegetative method of reproduction, however,* is the *sexual.* The essential feature here is *the union of two specialized sexual cells, or gametes, to form a single cell, the fertilized egg or zygote, from which a new individual develops.* To insure the successful consummation of this process is the function of a great variety of reproductive structures throughout the plant kingdom. These in the higher plants we call the flower, fruit, and seed. We are still uncertain as to what notable advantage is gained through this process of sexual union which should make it so common among plants. There is evidence in some cases that an increase in vigor characterizes the offspring of a sexual union, but just how valuable this advantage is we do not know, for there exist many very successful species which now depend wholly or in great part upon asexual reproduction.

In the present discussion we shall consider only the higher seed plants and shall reserve a study of reproduction in the lower members of the plant kingdom for later chapters.

The Flower.—Seed plants are characterized by the possession of a rather complex reproductive apparatus known as the *flower.*

This consists typically of those structures intimately concerned with the development of the sexual cells, together with others which contribute indirectly to the success of the process of reproduction (Figs. 97 and 98).

Stamens and Pistils.—The essential organs of the flower are the *stamens* and *pistils*. Each stamen bears an *anther* or pollen sac,

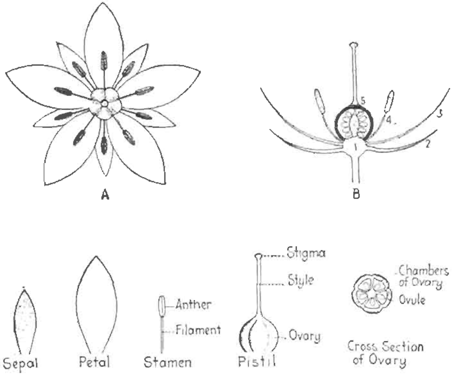

FIG. 97.—The structure of the flower of a dicotyledonous seed-plant (diagrammatic). *A*, face view of the flower, showing its calyx of five sepals, its corolla of five petals, its ten stamens, and its pistil. *B*, longitudinal section, showing the relations between the parts. 1, receptacle. 2, calyx. 3, corolla. 4, stamen. 5, pistil, with ovary cut lengthwise.

and within this sac are produced a great number of minute, single-celled *pollen grains* (Fig. 99), from the contents of each of which two male gametes ultimately develop. The anther is commonly supported by a stalk or *filament*. The pistil consists of a closed chamber, the *ovary*, at the top of which is the *stigma*, a structure adapted to catch and hold the pollen grains. The stigma is often supported by a stalk or *style*. In the ovary are borne the *ovules* or potential seeds, within each of which is a female gamete or egg. The fertilization of an egg by a male gamete starts the series of processes which result in the development of the ovule into a seed.

Chromosome Reduction.—Certain noteworthy differences occur between the cell division which preceeds the formation of the gametes and those which we have studied in the ordinary

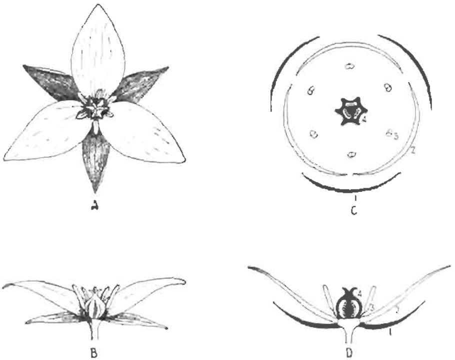

FIG. 98.—The structure of a flower of a monocotyledonous seed-plant (*Trillium*). *A*, face view of the flower showing calyx of three sepals; corolla of three petals; 5 stamens, and the pistil. *B*, side view of the flower with one petal and one stamen removed. *C*, a transverse diagram of the flower, the sepals and ovary walls black, the petals, stamens and ovules outlined. *D*, a longitudinal diagram of the flower. 1, sepal. 2, petal. 3, stamen. 4, pistil.

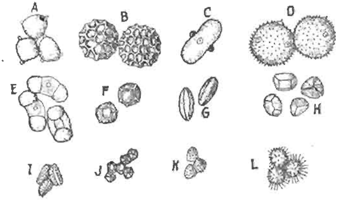

FIG. 99.—Pollen grains of various types. *A*, *Circaea*. *B*, *Cobaea*. *C*, *Morinda*. *D*, *Cucurbita*. *E*, *Pinus*. *F*, *Dianthus*. *G*, *Gentiana*. *H*, *Corydalis*. *I*, *Nymphaea*. *J*, *Taraxacum*. *K*, *Buphthalmum*. *L*, *Hibiscus*.

vegetative tissues of the plant; and a knowledge of these differences is essential to a thorough understanding of the laws of

inheritance, which we shall later discuss. In this division the chromosomes, as they make their appearance out of the nuclear network, are grouped in pairs; and when division takes place, the members of each pair separate, one going to one of the newly formed nuclei and the other to the other. The splitting

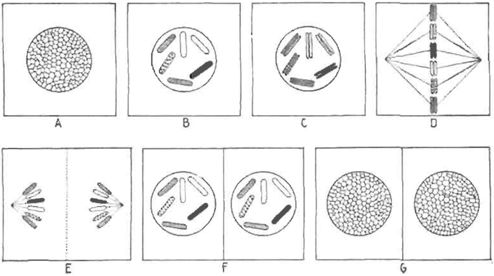

FIG. 100.—Diagram of mitosis in a ordinary body-cell. *A*, resting nucleus. *B* and *C*, prophases. *D*, metaphase. *E* and *F*, telophases. *G*, new cells. The separate chromosomes, each of which has an individuality of its own, are differently marked. It is evident that the chromatic material is divided exactly evenly between the two daughter cells. (*Modified from Sharp.*)

of chromosomes which occurs in ordinary mitosis (Fig. 100), and by which the chromosome number is maintained, *does not occur here*, and the resulting daughter nuclei (and the gametes derived from them) therefore contain only *half* the chromosome number found in the ordinary body cells of the plant. Such a division is accordingly known as a *reduction division* (Fig. 101). When the gametes later unite in fertilization, each contributes its quota of chromosomes, and in the fertilized egg the original chromosome number is thus restored and then persists throughout all the cells of the plant which develops therefrom. The essential differences between these two types of division are shown in the appended diagrams.

Perianth.—The pistil occupies the center of the flower, with the stamens in a circle around it; and outside of these, in turn, is the *perianth*, composed typically of two circles of parts. The inner one of these is the *corolla* or circle of *petals*. The petals are flat, somewhat leaf-like structures, usually conspicuous in color and rather delicate in texture, whose chief function is to attract

to the flower those insects which are important in effecting pollination. Finally, outside the corolla is the *calyx* or circle of *sepals*. These are usually green or greenish structures which protect the delicate inner organs of the flower while in the bud. All floral

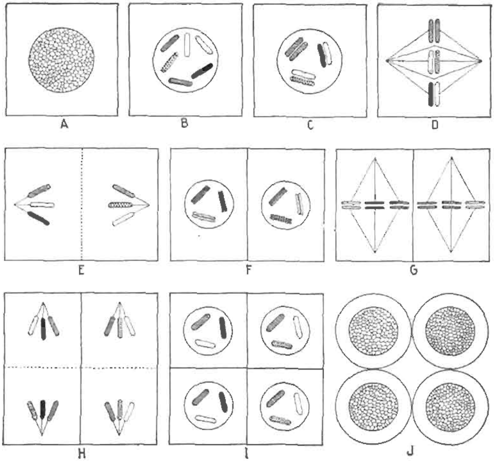

FIG. 101.—Diagram of the "reduction division", which occurs in the development of reproductive cells. Formation of a tetrad or group of four pollen grains. *A*, resting nucleus in the pollen mother-cell. *B*, the six chromosomes become distinct, each with an individuality of its own. *C*, these chromosomes group themselves into three pairs. *D*, the three pairs become arranged across the equator of the cell. *E*, the members of these pairs separate, three going to one pole and three to the other. *F*, two new cells are formed, each of which has just *half the chromosome content of the mother-cell, as a result of this reduction* division. *G*, *H*, and *I*: these cells each divide in two normally, producing four cells each with the reduced chromosome number. *J*, four pollen grains which have thus arisen from the pollen mother-cell. (*Modified from Sharp.*)

parts are attached to the *receptacle* or enlarged tip of the flower stalk.

Variations in Floral Parts.—These four groups of organs exhibit such great differences in the number, shape, size, color, texture and relative position of their parts as to give the flower a

far greater range of structural diversity than the other organs of the plant, and we therefore depend upon the flower very largely for those characters which distinguish genera and families of plants from one another.

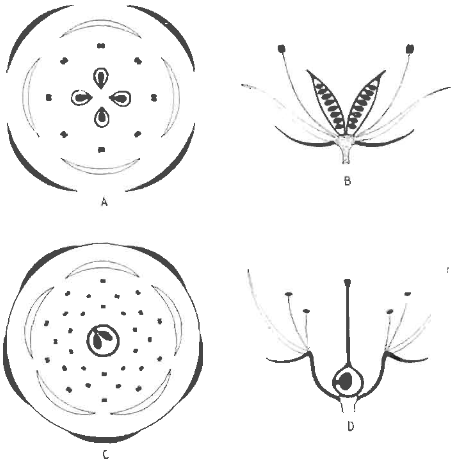

FIG. 102.—Diagrams of various types of flowers. The transverse diagrams show the numbers of parts and the relations between the members of the same circle of parts. The longitudinal diagrams show the relations between the various circles. Receptacle dotted, petals and filaments outlined, and other structures solid black. *A* and *B*, transverse and longitudinal diagrams of the flower of the Stonecrop (*Sedum*). Sepals, petals, stamens and pistils are all free from one another. They are all attached directly to the receptacle, or are *hypogynous*. Each ovary is simple. *C* and *D*, Cherry (*Prunus*). The sepals are united into a *gamosepalous* calyx but the petals and stamens are all separate. The corolla and the stamens are attached directly to the calyx, or are *episepalous*. The ovary has but one chamber, in which are two ovules.

In number, the circles may differ considerably. Among some of the more primitive orders there are several separate pistils (Fig. 102, *A*), but this part of the flower is more often single, at least as far as its ovary is concerned, although from the number of stigmas or of chambers in the ovary we have reason to

believe that in many cases there has been a fusion of several pistils, and that the many-chambered ovary is thus a *compound* structure (Fig. 103). The stamens are often the most numerous of the floral parts and are generally free from one another, although in some families they may be partially fused together. The petals are usually fewer than the stamens and rarely exceed

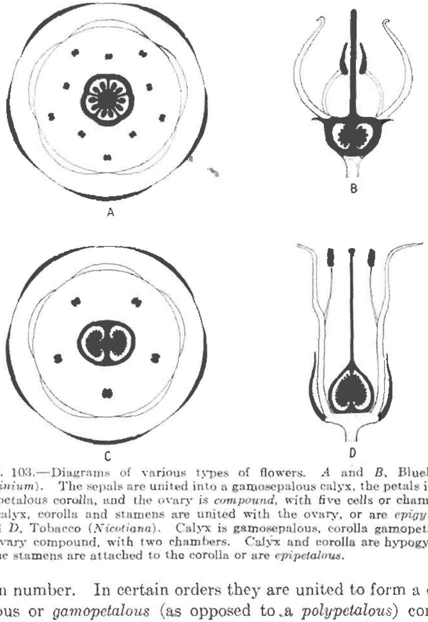

FIG. 103.—Diagrams of various types of flowers. *A* and *B*, Blueberry (*Vaccinium*). The sepals are united into a gamosepalous calyx, the petals into a gamopetalous corolla, and the ovary is *compound*, with five cells or chambers. The calyx, corolla and stamens are united with the ovary, or are *epigynous*. *C* and *D*, Tobacco (*Nicotiana*). Calyx is gamosepalous, corolla gamopetalous and ovary compound, with two chambers. Calyx and corolla are hypogynous but the stamens are attached to the corolla or are *epipetalous*.

ten in number. In certain orders they are united to form a continuous or *gamopetalous* (as opposed to a *polypetalous*) corolla (Fig. 103). The sepals are generally of the same number as the petals and, like them, may sometimes be fused together into a *gamosepalous* (as opposed to a *polysepalous*) calyx (Fig. 102). Not only are the members of one circle sometimes joined together,

but two entire circles may even be united. The corolla is sometimes attached to the calyx and is thus *episepalous* (Fig. 102, *D*). Similarly, the stamens may be *epipetalous* (attached to the corolla Fig. 103, *D*) and the calyx *epigynous* (attached to the ovary, Fig. 103, *B*) and so on. In shape, floral parts vary enormously. In

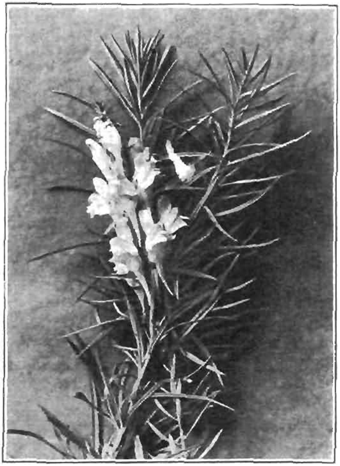

FIG. 104.—An irregular flower, the toadflax (*Linaria vulgaris*). The corolla has two lips, which are spread apart by the bee as he enters in search of the nectar, which is secreted by a gland or *nectary* at the end of the long spur.

the higher plant groups, too, some of the sepals, petals or stamens are different from the rest, with the result that an unsymmetrical or *irregular* flower (Figs. 104 and 240) is produced, as opposed to the more primitive *regular* type (Figs. 97, 98, and 109). In color, flowers range through practically the entire spectrum, except that green is comparatively rare in the corolla. In size there is also great diversity, although flowers more than a decimeter in diameter are rare. In texture, flowers are generally soft except for the calyx, the firmness of their parts being produced by

turgidity of the cells rather than by skeletal tissues. In certain cases, however, notably in the grasses and allied families, the perianth segments have become hard, dry, and chaffy.

Any one, or more than one, of the floral circles may sometimes be absent. If both calyx and corolla are missing the flower is

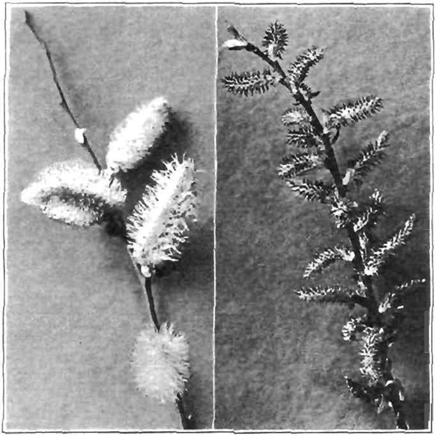

Fig. 105.—Catkins from a male plant of willow (*Salix*) showing the masses of stamens.

Fig. 106.—Catkins from a female plant of willow. The prominent pistils can readily be seen.

said to be *naked*. If it is either the stamens or the pistil which is absent, the flower is *unisexual* and is called either "male" or "female" according to the structures which it possesses. If both male and female flowers are distinct from one another but are on the same plant (as in corn, birch and many others) the plants are said to be *monoecious*; if the two sexes are on separate plants (as in the willow, Figs. 105 and 106) the species is termed *dioecious*.

In studying the evolution of floral parts, evidence has been obtained that the sepals, petals, and probably the stamens and

units of the pistil are morphologically leaves; and that the earliest floral type was perfectly regular, with its various parts rather numerous and with no fusion whatever between circles or between members of the same circle.

Inflorescence.—The arrangement of flowers on the plant is known as the *inflorescence.* The flowers may be *solitary*, arising from the ground, or singly in the axils of the leaves (Figs. 233

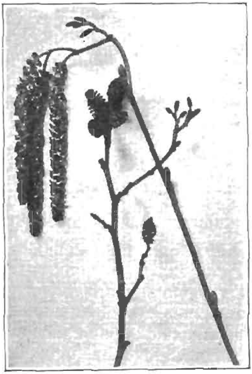

FIG. 107.—Wind-pollinated flowers of the alder (*Alnus*). The long catkins are groups of male flowers just ready to shed their pollen. The smallest catkins are composed of female flowers, their stigmas ready to receive the pollen blown through the air. The woody cones of last year, which developed from the female catkins and have shed their seed, are also shown.

and 240); or the leaves may be reduced to small *bracts*, the internodes shortened, and the flowers thus grouped into definite clusters. Such clusters are of various types as to shape and arrangement, the commonest among them being the *raceme* (Fig. 234), *spike*, *head* (Fig. 236), *umbel* (Fig. 235), *corymb*, *panicle, and cyme.*

Pollination.—*The first step in the accomplishment of reproduction is the transfer of pollen from the anthers to the stigma,* a process known as *pollination.* At about the time the flower unfolds, the anthers open and liberate the pollen grains. In rare cases the stigma lies so close to the anthers that the pollen is

transferred thereto directly, and this may sometimes happen even before the flower opens. In the great majority of cases, however, this transfer is brought about by some external agency, and pollen from the flowers of one plant is thus frequently carried to the flowers of another.

The two most important agencies in effecting pollination are the wind and insects. Wind-pollinated or *anemophilous* flowers (Figs. 107 and 237) are prominently exposed on the plant but are generally small, inconspicuous and unisexual, possessing a poorly-developed perianth, abundant dry and light pollen, and feathery stigmas. Insect-pollinated or *entomophilous* flowers (Figs. 104, 109, 240, etc.), on the other hand, are conspicuous or possess marked odor, and are characterized by a well-developed corolla, pollen grains which tend to adhere in masses, stigmas which are sticky, and in many cases by the presence of *nectaries* secreting a sugary liquid. The insect is guided to the flower by its color or odor and visits it either to secure nectar, the source of honey, or pollen, the source of "bee bread". Pollen readily adheres to the hairy bodies of these insects, and as it is thus carried about from flower to flower it often comes in contact with a stigma, to the sticky surface of which it is transferred. Insects belonging to the order Hymenoptera (the bees and their allies) are more important than any others in effecting pollination.

In many cases we have evidence that offspring which arise from a *cross*, or union of sexual cells contributed by two *different* parents, are superior in vigor to those in which both gametes came from the same plant. Perhaps in response to this fact, there are an enormous number of devices among flowering plants which tend to insure *cross-pollination*, or the transfer of pollen from one flower or plant to another, and to prevent *self-pollination*, or the transfer of pollen from anther to stigma of the same flower. Anthers and stigmas, for example, may ripen at different times, with the result that the anthers liberate their pollen either before the stigma of the same flower is ripe for pollination or after it has become no longer receptive. In many cases, also, pollen from another plant is better able to effect fertilization than the plant's own pollen; and in extreme instances the plant may be actually *self-sterile*, its own pollen having no effect whatever upon its stigma. More striking than these methods, however, are the multitude of structural devices in entomophilous flowers whereby self-pollination through insect agency is rendered diffi-

cult or impossible and cross-pollination made easy. This is sometimes accomplished by *floral dimorphism* (Fig. 108), in which there are two types of flowers, so constructed that the points

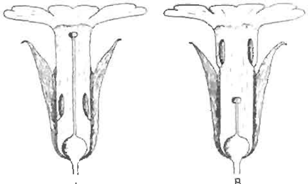

FIG. 108.—Dimorphic flowers of Chinese primrose (*Primula sinensis*). *A*, flower with long style and with stamens attached low in the tube of the corolla. *B*, flower with short style and with stamens in the throat of the corolla.

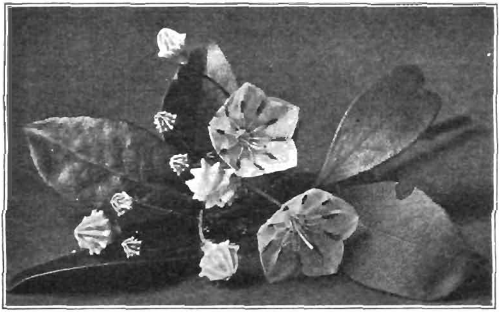

FIG. 109.—Flowers of the mountain laurel (*Kalmia latifolia*). The anthers are held in little pockets in the corolla, but the disturbance of the flower, as by the alighting of an insect upon it, will release the stamens and they will snap upward sharply, thus covering the insect with pollen.

where the anther and stigma touch the insect's body are exactly reversed, with the result that the pollen of one is apt to reach the stigma of the other. More common are the various and often intricate devices in which hairs, springs (Fig. 109), traps, and other agencies are employed. These reach their highest develop-

ment in such families of irregular-flowered plants as the legumes and orchids, and have long excited the curiosity and admiration of naturalists.

Fertilization.—Pollination, however, is only a step toward the union of male and female gametes which we know as *fertilization*

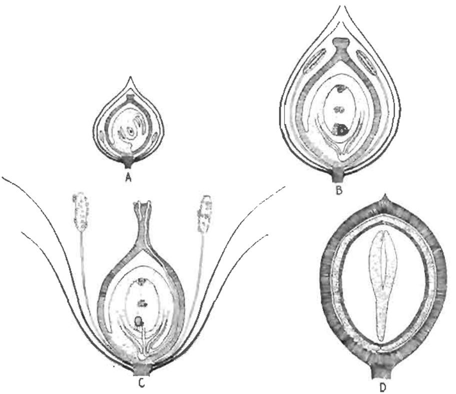

FIG. 110.—The process of seed-production in a flowering plant. Longitudinal diagrams of flower and fruit, the calyx and corolla solid black; the ovule, seed-coats and embryo dotted, and the ovary wall, style and stigma lined. *A*, young bud, the stamens and the single ovule beginning to develop. *B*, bud ready to unfold. The embryo-sac within the ovule is fully developed and the egg (below) and double endosperm nucleus (in center) are ready for fertilization. *C*, fully opened flower. The anthers have burst and pollination has taken place, pollen grains being transferred to the stigma. Two grains have germinated, and the pollen-tube from one of them has penetrated the style, entered the ovary, passed through the micropyle of the ovule and discharged its contents—the two male gametes—into the embryo-sac. Double fertilization is taking place, one male gamete uniting with the egg and the other with the endosperm nucleus. *D*, ripe fruit. Sepals, petals and stamens have dropped off; the ovary wall has hardened into the pericarp; the micropyle has closed; the integuments have become seed coats and the ovule has developed into the seed. The embryo, in the center of the seed, has grown from the fertilized egg, and the endosperm surrounding it (shown in white) from the endosperm nucleus.

(Fig. 110). Although the pollen grain is a single cell, it is not the male gamete. At about the time of pollination, the nucleus of the grain divides into two, one of which, the *tube-nucleus*, remains free in the cytoplasm. The other nucleus surrounds itself with a

mass of cytoplasm of its own, sometimes with a separate wall, and is known as the *generative cell.* Shortly after the pollen has reached the stigma the thick wall of the pollen grain bursts at one point and out of the grain proceeds a thin-walled *pollen-tube.* Near the tip of this moves the tube-nucleus, followed by the generative cell (Fig. 111). This tube bores through the tissues

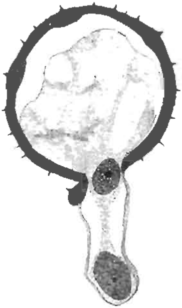

FIG. 111.—Germinating pollen of squash. The pollen grain has burst and a pollen tube is starting down through the style. Near the end of the tube is the tube nucleus. Some distance behind is the generative cell, from which are later developed the two male cells. (*From A. I. Weinstein*).

of the style and carries the contents of the pollen grain down into the ovary and to the mouth of an ovule (Fig. 110, *C*). Meanwhile the generative cell divides into two *male cells,* which are the true male gametes.

By this time the ovule has become prepared for fertilization. It possesses one or two coats or *integuments,* later developing into the seed-coats, which cover it except at one point, the mouth or *micropyle.* Here the pollen-tube usually enters. Inside the integuments is a thin nutritive layer, the *nucellus.* Within this, in turn, and ordinarily occupying the whole central portion of the ovule, is the *embryo-sac.* This is a small, sap-filled cavity with three cells at each end and a naked nucleus, the *endosperm nucleus,* near its center. The three cells at the end of the sac farthest from the micropyle play no part in fertilization or seed development. Of the three at the micropylar end, however, one is usually distinguishable by its greater size and is the female

gamete or *egg*. *With the nucleus of this egg cell fuses one of the male gametes which has come down the pollen tube* (Fig. 110, C). This union produces the *fertilized egg*, and *from this single cell* develops the entire embryo of the seed and thus the young plant which grows therefrom. This fertilized egg, in which are combined the protoplasm of the two parents, is the *sole* direct link between parents and offspring; and only across this exceedingly narrow bridge are characteristics transmitted by inheritance from one generation to the next.

The fertilization of the egg by a male cell is not the only cell union which takes place at this time, for the other male cell fuses with the endosperm nucleus (Fig. 110, C), and from the cell thus formed arises the endosperm or food-storage tissue of the seed.

Fertilization effected by gametes from the same plant is known as *self-fertilization;* that by gametes from different plants as *cross-fertilization.*

Seed Development.—After fertilization has been effected, the petals and stamens drop off and the ovule gradually develops into the *seed* (Fig. 110, *D*). Various changes accompany this process. The whole structure grows markedly in size and the integuments increase in thickness, become hard and woody, and close over the micropyle. In many seeds a considerable mass of *endosperm* or food-storage tissue is developed, but in others this is much less abundant. Within the endosperm is the *embryo* or young plant, which has developed from the fertilized egg. In dicotyledonous plants (p. 360) the embryo is differentiated into three main portions; the *hypocotyl* or primitive stem and root, its tip directed toward the micropyle; the two seed-leaves or *cotyledons,* attached to the upper end of the hypocotyl, and the *plumule* or bud, inserted between the cotyledons (Fig. 112). The cotyledons may be very thick and serve entirely for food storage, as in the pea; they may be thin and leaf-life, serving as foliage leaves from the beginning, as in the morning glory, or they may combine both functions, as in the squash. In *monocotyledonous* plants (p. 364) endosperm is always well developed and the comparatively small embryo consists of a flat disc, the *scutellum* (which probably represents a single cotyledon) to the face of which are attached an upward-pointing, sheathed *plumule* or bud and a downward-pointing minature root or *radicle* (Fig. 113). The scutellum serves to absorb food from

the endosperm and to transmit it to the growing portions of the embryo.

The ripe seed is thus a structure in which the partially developed young plant, well protected and provided with an abundant supply of food for future growth, is able to pass through a more or less extended period of dormancy.

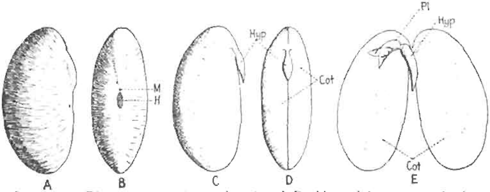

Fig. 112.—The structure of a seed. A and B, side and face views of a bean seed. C and D, side and face views of the embryo after the seed-coats have been removed. E, the two cotyledons spread apart, revealing the plumule within. M, Micropyle. H, Hilum. Cot., Cotyledons. Hyp., Hypocotyl. Pl., Plumule.

The Fruit.—The ripened ovary, together with its contents the seeds, and with any other structures intimately associated with these, is known as the *fruit*. The ripened wall of the ovary is

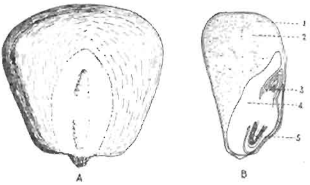

Fig. 113.—A kernel (grain or fruit) of corn. *A*, face view, showing outline of embryo in the middle. *B*, longitudinal section. 1, Pericarp and seed coat, fused. 2, Endosperm. 3, Plumule. 4, Scutellum or cotyledon. 5, Radicle. 3, 4 and 5 constitute the embryo.

called the *pericarp*. Fruits are various and many different types are recognized and named, but we shall mention here only the most common and important of them. Some are dry at maturity and split open. Such are the *capsule* (as in the lily), which arises from a compound ovary, and the *pod* (as in the

bean), which arises from a simple or single-chambered one. Others are dry but do not split open. Such are the *achene* (as in the buttercup), the commonest type of single-seeded fruit; the *nut* (as in the hickory), in which the pericarp becomes hard and woody, and the *grain* (as in the corn), the characteristic fruit of the grass family, in which seed coats and pericarp are firmly fused. These single-seeded fruits are often mistaken for seeds. Many fruits become fleshy, at least in part. In the *berry* (as

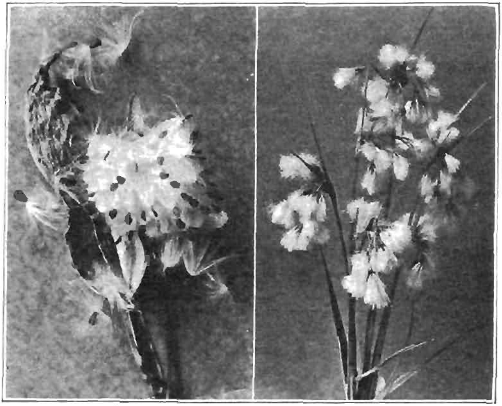

FIG. 114.—Seed dispersal by the wind. *A*, ripe fruit of the milkweed, *Asclepias*. Each seed is provided with a tuft of feathery hairs, which aid in the dispersal of the seeds by the wind. *B*, fruits of the cotton-grass, *Eriophorum*. Each tuft in the picture is composed of a group of single-seeded fruits, attached to each of which is a cluster of long, cottony hairs.

in the blueberry), the entire fruit is so except the seeds, which have thick coats. In the stone fruit or *drupe* (as in the cherry), the outer part of the pericarp is fleshy, but the inner portion, enclosing the seed, is a hard and woody "stone." In the *pome*, represented by such fruits as the apple and pear, it is the receptacle, grown around and enclosing the fruit, which becomes fleshy, the pericarp being represented here only by the tough membranes of the core.

Seed Dispersal.—It is obvious that to leave successful offspring a plant must not only develop seeds but must provide for their dispersal; and in bringing this about, almost as great a variety of adaptive devices are employed as there are to insure cross-pollination. Dependence is placed upon various agencies, but chiefly the wind and animals. Many seeds or even entire fruits are light and provided with wings or tufts of long hairs, so that they present a large surface for the wind to catch, and are often

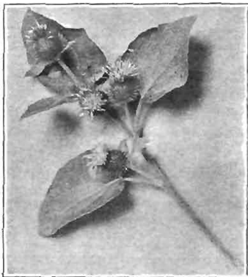

FIG. 115.—Flower clusters of the burdock (*Arctium*). The bracts which surround the cluster are stout and hooked, and thus aid in the dispersal of the fruit.

FIG. 116.—Conspicuous berries of the baneberry (*Actaea*).

wafted many miles (Fig. 114). In the case of the various "tumble weeds" the entire plant breaks off at the base of the stem and is rolled along over the ground by the wind. Other fruits and seeds develop hooks (Fig. 115), spines, or sticky secretions which enable them to adhere to the fur of animals or the feet of birds and thus to be carried for long distances. In fleshy fruits, the fleshy portion or pulp is usually bright in color (Fig. 116) and is rendered attractive to animals by its taste. Birds are particularly important in the dissemination of the seeds of such fruits. In a few cases like the witch hazel, the fruit splits open with such force that the seeds are projected through the air for a considerable distance. The seeds and fruits of water and shore plants are usually dispersed by floating on the water and have been known to travel thus for hundreds of miles.

Seed Germination.—The seed remains dormant until a favorable environment appears, when the embryo begins to grow and the seed is said to *germinate* (Fig. 117). The conditions necessary for germination are a plentiful supply of water and oxygen and a moderately high temperature. When these are fulfilled, metabolism begins vigorously in the embryo and in the cells of the endosperm. Water is absorbed in large quantities

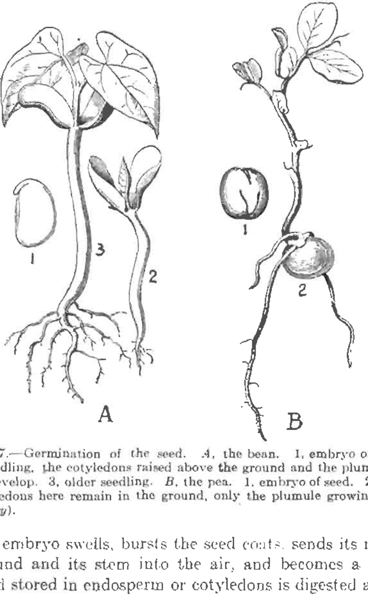

FIG. 117.—Germination of the seed. *A*, the bean. 1, embryo of seed. 2, young seedling, the cotyledons raised above the ground and the plumule beginning to develop. 3, older seedling. *B*, the pea. 1, embryo of seed. 2, seedling. The cotyledons here remain in the ground, only the plumule growing upward. (*From Gray*).

and the embryo swells, bursts the seed coats, sends its root into the ground and its stem into the air, and becomes a *seedling*. The food stored in endosperm or cotyledons is digested and used for the development of new organs. It is generally sufficient in amount to provide for the growth of the seedling to a point where the latter can begin to manufacture its own food. Indeed, as soon as the young stem and leaves get above the ground they

turn green and commence photosynthetic activity, soon supplying an abundance of food which insures the rapid development of the plant from the seedling stage to maturity, at which point the cycle of reproduction is complete.

QUESTIONS FOR THOUGHT AND DISCUSSION

538. Is asexual reproduction commoner in animals or in plants? Explain.

539. Give an example of a plant which commonly reproduces itself asexually.

540. What advantage is it to the potato to reproduce by tubers rather than by seeds? What disadvantage is there in this process?

541. What advantages, aside from the one mentioned in your text, may sexual reproduction have over asexual multiplication?

542. What connection do you think there has been between the stationary habit so characteristic of plants and their reproduction by means of flowers?

543. The petals of a flower usually drop off after seed is set but the sepals commonly remain. Of what advantage are these two facts to the plant?

544. Pollen grains are often roughened. Explain.

545. Can you suggest what makes the pollen grain germinate and why it grows down the style directly to the ovule?

546. Why is pollen generally spoiled if it is wet by the rain?

547. What effect does the weather at apple-blossom time have upon the size of the subsequent apple crop?

548. Do you think that the earliest seed plants were pollinated by wind or by insects? Why?

549. What advantages and what disadvantages are there in wind-pollination?

550. Trees which are wind-pollinated usually flower early in the spring. Explain.

551. The flowers of most coniferous trees are borne near the ends of the branches, and the flowers of grasses are usually raised up on a tall spike. Explain these facts.

552. What advantages and what disadvantages are there in insect-pollination?

553. The corollas of most flowers are some other color than green. Explain.

554. Why are low-growing plants almost always pollinated by insects?

555. *Alpine flowers are usually brilliant in color or otherwise conspicuous.* Explain.

556. Night-blooming flowers are usually white. Explain.

557. Low-growing and inconspicuous flowers are often very fragrant. Explain.

558. *In many plants, the flowers are arranged in clusters. Of what* advantage is this to the plant?

559. In most flower clusters, the flowers open a few at a time rather than all at once. Explain.

560. Are solitary flowers usually larger or smaller than those which occur in clusters? Explain.

561. Do you think that bees are attracted to flowers by the same odors which are attractive to human beings? Do you think that the same holds true for flies? Explain.

562. Most flowers do not exceed a decimeter in diameter and the great majority are very much smaller. Can you explain why flowers are commonly not larger than this?

563. Many flowers are so constructed as to admit bees readily but to exclude ants. What does the plant gain by this?

564. It is a general rule that plants rich in nectar tend to have hairy stems and flower stalks. Explain.

565. In many plants, the removal of the stamens as soon as the bud opens often causes the flower to remain in bloom longer than it would if the stamens were left attached. Explain.

566. *What means of dispersal have plants aside from the dispersal of* their seeds? Give examples.

567. Other things being equal, which type of plant will become dispersed more rapidly, a tree or an herb? Explain.

568. What advantage is it to a berry-bearing plant to have its fruits brightly colored?

569. What color prevails in unripe fruit? Explain.

570. Why is green such an uncommon color among ripe berries?

571. Fleshy fruits usually have stony seeds or a stony layer around the seed. Explain.

572. Of what use to the plant is the fleshy food stored in such a fruit as that of the apple?

573. The flower stalks of the dandelion elongate after the seeds have been formed. Of what advantage is this to the plant?

574. As a general rule, how tall are plants in which the fruit bears hooks or similar structures?

575. Just what part of the seed develops into the new plant?

576. Why does cracking or chipping the shell of a hard-shelled fruit or seed often hasten its germination when planted?

REFERENCE PROBLEMS

86. What relation has there been between the evolutionary history of insects and of flowers?

87. What flowers are there which depend on flies rather than on bees for pollination? How do they differ from bee flowers?

88. Does a bee visit all kinds of flowers, one after the other, on the same day, or does he confine himself to one species? Explain the importance to plants of this behavior.

89. Some varieties of strawberries will set seeds when planted by themselves. Others will not. Explain.

90. One corn stalk alone in a field is apt to produce few or no seeds. Why?

91. Cucumbers and melons will not fruit naturally in greenhouses, at least in winter. Why not?

92. What is *Xenia?* Of what economic importance is it?

93. Give examples (other than those in the text) of a capsule, a pod, an achene, a nut, a grain, a berry, a drupe, and a pome.

94. Name three cultivated fruits which are essentially seedless

95. Give the derivation of the following terms and explain in what way each is appropriate:

Calyx	Petal	Hypocotyl
Corolla	Stamen	Micropyle
Perianth	Pistil	Cotyledon
Sepal	Ovule	Plumule

CHAPTER XI

HEREDITY AND VARIATION

As a result of the process of reproduction which we have described in the preceding chapter, a continuous succession of new individuals arises. One of the most remarkable features of this reproductive activity is that each of these new individuals bears a very close resemblance to its parents. The offspring of wheat plants are always wheat plants and nothing else; and the offspring of oak trees are always oaks. Furthermore, any particular kind or variety of wheat or of oak will produce (under proper conditions) plants of that kind or variety. This tendency for offspring to display the particular characteristics which distinguish their parents is called *heredity*.

Heredity.—We have already noted the exceedingly narrow physical bridge—the reproductive cells or *gametes*—which connects one generation with the next. To its offspring, one parent contributes a single male cell and the other parent a single egg cell, and out of the fertilized egg arising from the fusion of these two gametes, the new plant develops (Fig. 118). It is evident, therefore, that the parental characteristics must in some way be transmitted in the protoplasm of these tiny sexual cells. Any actual plant character (such as redness of flower or tallness of stem) obviously cannot be found in these cells; but something representing it, and capable of producing it in the new plant, must be there. This "something"—we are still ignorant of its real nature—is called the *factor* or *gene* for the character in question. In a wheat plant, let us say, the height and strength of the stem, the shape and texture of the leaf, the number of spikelets in the head, the shape, color and surface of the glumes, the weight of the kernel, the character of the grain, the yield of seed, the resistance of the plant to cold, drought and disease, together with a host of other characteristics, have all been shown to be clearly inheritable. It is evident that in every male gamete and in every female gamete there must be a factor which represents each of these characteristics and which thus determines the

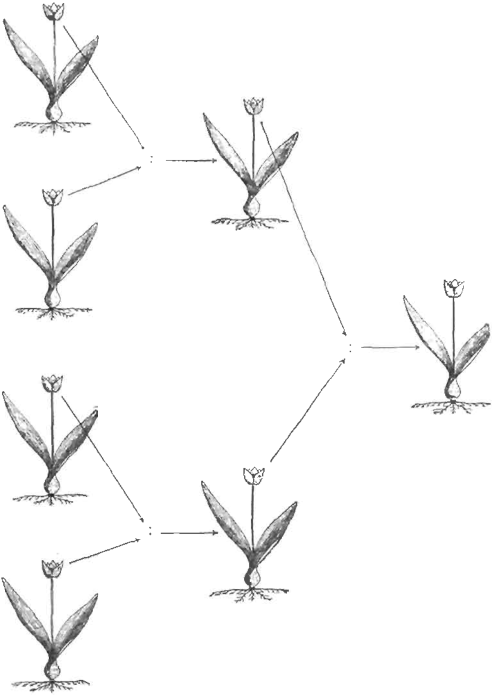

FIG. 118.—The narrow hereditary bridge. The plant at the right receives from each of its parents only one minute sexual cell, a male gamete from one and a female gamete from the other. The parents, in turn, receive from each of the grandparents but one sexual cell. Thus the bridge which connects one generation with the next, and over which the entire inheritance must pass, is an exceedingly narrow one. The actual gametes are very much smaller, both actually and in proportion to the size of the plant, than the dots by which they are here represented.

particular kind of wheat plant which is to be produced. These minute particles of protoplasm, into which so much is packed and out of which so much emerges, are certainly among the most remarkable bits of matter in existence.

FIG. 119.—Variation in number, form, and size of leaflets in the blue elderberry. *Sambucus glauca*. (*From Babcock and Clausen*).

Variation.—Close as the resemblance is between parent and offspring, however, it is almost never an exact resemblance. Any individual plant or animal, if studied closely enough, will be

found to differ somewhat, even though very slightly, both from its parents and from its fellow offspring. These differences are known as *variations* (Figs. 119 and 120) and their presence brings about that variability which is so characteristic of all living things.

Laws of Inheritance.—The close attention given to the problems of breeding by those who have been responsible for the steady improvement of our domesticated animals and plants through the

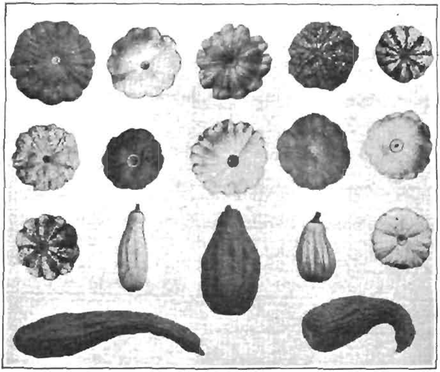

FIG. 120.—Variation in color, shape, size, and surface in the fruit of the summer squash. All of these types may appear among the descendants of a single individual.

centuries has been rich in practical gains, but it has contributed little to an understanding of inheritance beyond a recognition of these two main facts of heredity and variation. Man has long known that "like begets like" and that offspring differ among themselves, and he has used this knowledge in choosing the best individuals and breeding from them. In this way breeders have made steady improvement, but this improvement has been largely due to sharp-sightedness in seizing upon favorable variations rather than to a fundamental understanding of inheritance which would enable the breeder to control the process and predict its results. Within the last century, however, and particularly within the last twenty years, notable advances have been made

in our knowledge, and we are now beginning to see that there are indeed *laws of inheritance*, an understanding of which will enable us to raise the art of breeding from clever but uncertain guesswork to such a firm scientific basis as that upon which chemistry and physics now rest. An investigation of these laws is the province of the modern science of *genetics*.

Inheritance of Acquired Characters.—We have learned, for example, that all variations do not behave alike in inheritance. Some are due to factors embodied in the constitution of the

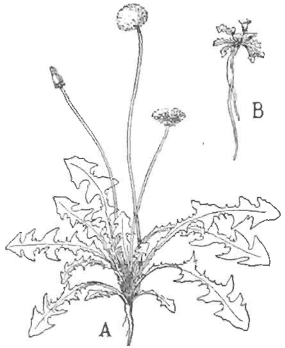

FIG. 121.—Variation produced by the environment. *A*, Plant of the dandelion (*Taraxacum*) grown in a lowland garden. *B*, Portion of the same plant grown in an alpine garden, under relatively unfavorable conditions. (*From Bonnier*).

gametes and may thus be transmitted from one generation to the next. They are clearly inheritable and are the "raw material" with which the breeder may work. Other variations, and among them many important ones, result from the direct action of the environment upon the plant body during its growth and are apparently never transmitted to offspring. Such "acquired" characters are the increased size and vigor which result from growth in rich soil (Fig. 121), the thick and heavy leaves developed by many plants when exposed to bright sunlight, the galls and other malformations resulting from insect or fungus attack, the stunting effect of overcrowding, and many others. These varia-

tions merely affect the individual and do not reappear in the offspring unless the particular environment which has caused them persists. Acquired variations of this kind are of particular interest to the farmer or to anyone who is concerned with plant culture, since they can readily be controlled by a proper manipulation of the environment; but the breeder and the student of inheritance must learn to recognize them and to realize that they are quite valueless for his purposes. Good care and cultivation will bring out the best that there is in a poor race of plants but they can never change a poor race into a good one.

Mendel's Law of Inheritance.—It is therefore only with those characters which are clearly inherited that we are here concerned. As we study their behaviour in the passage from generation to generation we notice many apparent irregularities. The same parents will transmit different characters to their different offspring. Sometimes a particular parental character will fail to appear in the offspring at all. In other cases the offspring will develop characters possessed by neither of its parents but sometimes found in a more remote ancestor. It is these facts which geneticists are endeavoring to explain and to reduce to definite laws. The most notable of these laws, and the one which is the basis of our modern understanding of inheritance, is that formulated by Gregor Mendel (Fig. 122), an Austrian monk, in 1866. The great importance of his work was ignored at the time and was not recognized until 1900. Since that date a large number of investigators have diligently studied the applications of "Mendelism" in the inheritance of a wide variety of animals and plants, and although our advancing knowledge has resulted in many amplifications and interpretations of this law, it still remains fundamentally intact as the cornerstone of genetics.

In his cloister garden Mendel studied inheritance in peas, making hybrids between different types and studying the results from generation to generation. His method of attack on the problem differed in several important ways from that of previous workers. First, in his crosses between contrasting types Mendel would single out a particular character of the plant and follow out its behaviour by itself, rather than trying to study the whole complex individual at once. In this way the inheritance of flower color, of seed color, of seed surface, of plant height, and of several other characteristics of the garden pea were investigated. Second, he kept accurate pedigree records, making sure that he

knew the exact ancestry of every individual plant and the characters displayed by each of its ancestors and descendants. This method involves much care and pains, both in making artificially the particular pollinations desired and in preventing all pollinations by such uncontrolled agencies as insects and the wind, and the labor of keeping the records is often very great.

FIG. 122.—Gregor Johann Mendel, 1822–1884. (*From Genetics, by permission*).

Mendel's method is now almost universally adopted, however, by students of inheritance. Third, in each generation where contrasting characters appeared (both red flowers and white ones in the offspring from a single cross, let us say) he carefully *counted* the number of individuals of each type and thus obtained a mathematical statement of the facts. In short, Mendel applied the true *experimental* method to the problems of heredity.

The results derived by this novel and painstaking method of investigation were carefully reported by Mendel and his interpretations thereof have come to be known as Mendel's Law. This law, however, is not a single proposition but really a series of distinct principles. Its important points we shall now briefly discuss.

Unit Characters.—As a general result of his hybridization experiments, Mendel observed that the plant seems to behave in

inheritance as though it were an aggregation of independent and separable characteristics, each of which is perfectly distinct and may exist with any combination of other characters in a given individual. These traits he called "unit characters". We *now* know that the expression or appearance of these characters may vary considerably under different conditions and that the real unity lies rather in the underlying *factor* than in the visible (and perhaps variable) character which it produces. The essential point, however, is that the organism, so far as its behaviour in inheritance is concerned, seems to be made up of distinct and independent units. Purple flower color in peas, for example, is such a unit, and may be associated with either yellow or green seed color, wrinkled or smooth seed surface, tallness or dwarfness of vine, and so on. A skilful breeder may thus combine and rearrange the characteristics of his plants almost at will.

Dominance.—Mendel's studies also brought out the fact that when plants which are dissimilar in a given feature (such as flower color, let us say) are crossed, the two characters thus brought together differ markedly in ability to express themselves in the resulting hybrid plant. When a pure purple-flowered plant is crossed with a pure white-flowered one, for example, *all* the offspring resemble the purple parent in their flower color. Such a character as purple flower color in peas Mendel therefore termed *dominant* and one like white flower color, which fails to appear in such hybrid offspring, he called *recessive* (Figs. 123 and 126). *A pair of contrasting characters like these are known as allelomorphs.* All the characters studied by Mendel happened to show complete or almost complete dominance or recessiveness, but many instances have since been found where a hybrid plant resembles neither parent exactly with respect to a given character-pair but is more or less intermediate between them. Such cases of the incomplete or imperfect dominance of one character over another in the hybrid state are much more common than those in which dominance is complete. The essential fact to be emphasized, however, and one that is of great practical import, is that the *appearance* of a plant (or animal) does not necessarily indicate its ancestry or its genetic make-up. Dominance, partial or complete, may enable a hybrid or mongrel to masquerade as a pure or superior individual.

Segregation.—Of much more importance than this fact of dominance in the hybrid was Mendel's discovery of the manner in

which characters are transmitted to the second and later generations following a cross. The hybrid offspring arising from a cross between a plant of a purple-flowered race and one of a white-flowered race are, as we have said, all colored. In appearance they resemble rather closely the purple-flowered parents, but in most such crosses the hybrids are somewhat paler than the pure colored types. When two of these *hybrid* colored plants are crossed, or when one of them is self-fertilized (which amounts to the same thing genetically) both colored-flowered and white-flowered plants appear in their offspring, the former constituting about three-fourths and the latter about one-fourth of the total number of individuals in the progeny. These white-flowered plants *breed perfectly true* when self fertilized, and purple flower color never appears in subsequent generations of their descendants when inbred. A part of the colored plants (approximately one-third of them) breed perfectly true to the purple color, none of their offspring, when inbred, possessing white flowers. The rest of the colored-flowered plants, however, (about two-thirds of them and thus about one-half of the total number of the offspring) resemble the hybrids in color and behave when self fertilized exactly as the hybrids did, producing offspring of which three-fourths are colored and one-fourth white. These facts are set forth diagrammatically in Fig. 123.* This separation and sorting out of characters which occurs in offspring of hybrid plants is known as *segregation*. The discovery and interpretation of segregation were perhaps the most important contributions which Mendel made to our knowledge of inheritance.

The essential character of segregation is shown in the behaviour of contrasting factors when they exist together in a hybrid individual. A factor transmitted through the gametes of one parent and a contrasting factor transmitted through the gametes of the other parent, come together and coexist in the cells of the hybrid offspring plant *without blending or losing their identity;* and when such a hybrid plant produces its own sexual cells, in turn, *the two factors become completely separated or segregated from one another,* each of the new gametes containing either the one or the other but *never both.* This is well illustrated by the example which we have been using. The factors for purple and for white flower color must both be present in the

* The first generation following a cross is technically known as the F_1 (first filial generation), the second as the F_2, the third as the F_3, and so on.

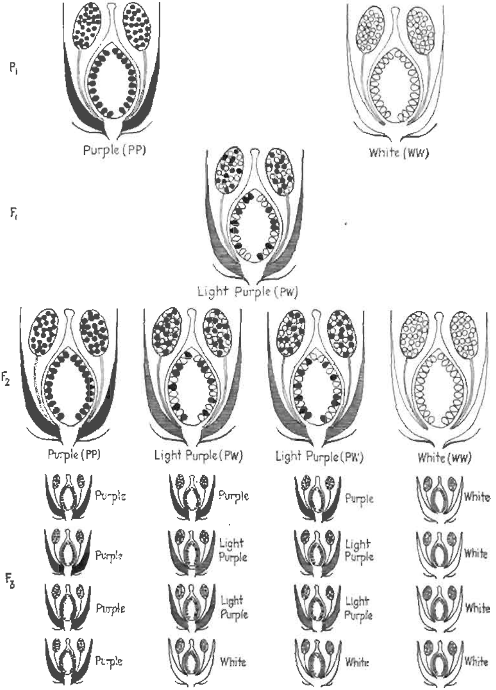

FIG. 123.—Mendel's Law of Inheritance. Longitudinal sections of flowers, showing color of corolla and genetic constitution of the male and female gametes, here represented by ovules in the ovary and pollen grains in the anther. The parents (P_1 generation) are in one case purple-flowered (*PP*) with the corolla represented solid black, and in the other, white-flowered (*WW*), with the corolla merely outlined. The gametes in the former all carry the factor for purple and are solid black; in the latter, all carry the factor for white. In the first hybrid generation or F_1 (*PW*), dominance of purple is not complete, for the corolla is colored but not as darkly as in the purple parent. Its color is represented by cross-hatching. Note that in the gametes, both male and female, about half

F_1 hybrid, though only the purple expresses itself visibly in the plant. Out of this purple hybrid, when self-fertilized, come some perfectly pure white plants which exhibit no trace of purple in their *descendants and some purples which exhibit no trace of white,*

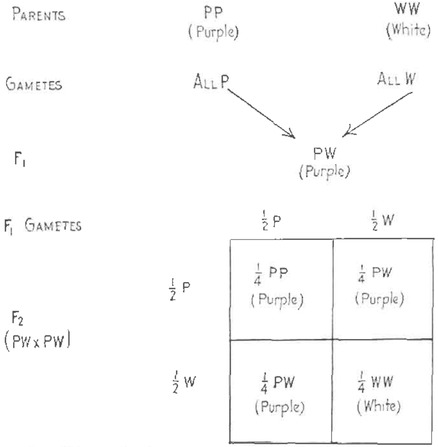

FIG. 124.—Diagram showing genotype (in letters), and appearance, of parents of the F_1, and of the F_2 in a cross between a purple-flowered and a white-flowered pea.

thus proving that the factors for these characters, which for a generation have been existing together in every cell of the hybrid plant, have now (in one-half of the individuals) become completely separated and have not produced the slightest effect on one another.

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carry the factor for purple and half for white, and that *none are "light purple"*. In the second hybrid generation or F_2, derived by self-fertilization of the F_1, about one fourth of the plants are purple, with all their gametes carrying the factor for purple; one half light purple, with about half their gametes carrying purple and half white; and one fourth white, all their gametes carrying white. The purple-flowered plants breed true to purple in the F_3, the white-flowered ones to white, and the light purple ones behave as did the light purple F_1, producing about one fourth purple, one half light purple, and one fourth white.

The Genotype.—The relation between this fact of segregation and the actual results which are obtained in crosses is perhaps best explained if we represent the factorial make-up of the plants and of their gametes by simple letters or formulas (Fig. 124) in somewhat the same way that Mendel did in his original work. Every individual is in a sense a *double* structure, since it arises from the union of two gametes and draws half of its inheritance from one and half from the other. If we let P represent the factor for purple flower color and W the factor for white flower color, our pure purple-flowered parent, which received the factor P from both of its parents, we might therefore represent by the formula PP; and our pure white-flowered parent in the same way by WW. This formula applies to every body cell of the plant. Of course it should be borne in mind that we are here representing only one of the great number of factor-pairs which are present in the constitution of the plant. In the cell divisions just preceding the formation of the gametes, there is a reduction by half in the amount of hereditary material contained in the nucleus* and every gamete produced now carries just *half* of each of the factor-pairs which composed the parent plant. The gametes of the purple-flowered parent in our illustration would therefore all be represented by the formula P and those of the white-flowered one by W. When these two plants are crossed and an egg, P, is fertilized by a male cell, W, (or *vice versa*), the genetic formula of the resulting hybrid plant is obviously PW. Since purple is almost completely dominant here, this plant *appears* purple-flowered, but in its factorial make-up (technically known as its *genotype*) there is a recessive factor for white. If dominance were absent and the hybrid were intermediate in appearance—pink, perhaps—we should of course still represent it by exactly the same genotype. When the two members of a given factor-pair are alike, (as in each of the parent plants between which this cross was made), the individual is said to be *homozygous* for the factor in question; when the two members are different (as in this hybrid) it is said to be *heterozygous.* Now the essence of the phenomenon of segregation lies in the fact that when this heterozygous individual produces gametes, *these* are not hybrid or

* The chromosomes of the nucleus are in all probability the actual bodies in which the genetic factors are carried, and we have shown (p. 187) that in the "reduction division" just preceding the production of gametes, the number of chromosomes in the nucleus is halved.

heterozygous at all, but half of them are P and half W. Thus the hybrid character of a plant cannot be carried by its gametes, which must be entirely one thing or entirely the other. The factors P and W, brought in from the original purple and white parents, have coexisted in the hybrid without influencing each other in the least and have now sharply parted company, or *become segregated.*

Mendelian Ratios.—In a cross between two of these hybrid F_1 plants (or in the case of a self-fertilization of one of them) the occurrence of the three-to-one ratio in the F_2 generation is thus easy to explain. Of the gametes of each parent, approximately half carry the factor P and half the factor W, so that in the perfectly free and random union which takes place between these gametes there are four possible combinations which may occur in the offspring produced. P male cells may fertilize P eggs, producing PP plants; P male cells may fertilize W eggs, producing PW plants; W male cells may fertilize P eggs, also producing PW plants, or W male cells may fertilize W eggs, producing WW plants. Each of these combinations, on the basis of pure chance, is apt to occur just as often as any other. Approximately one-quarter of the new generation, the PP plants, will not only look purple but will breed just as truly for this color as did their purple-flowered grandparent; approximately one-half, the PW plants, will also look purple (perhaps somewhat paler) but are of course heterozygous, and when selfed or when crossed among themselves will behave just as did their parent, the F_1 hybrid, and yield three colored-flowered plants to every white; and the final quarter, comprising the WW plants, will appear white and will breed as truly to this color as did their white grandparent (Fig. 124). The characteristic Mendelian ratio is therefore not three-to-one at all, but rather one-to-two-to-one. Of course it should be remembered that the results of actual breeding do not always display these ratios exactly, any more than in the tossing of coins or the throwing of dice there are always exact and predictable results. The ratios merely indicate what may be expected on the basis of probability.

Obviously when dominance is absent the F_2 generation will not include simply two sorts of plants, one three times as numerous as the other, but a third, as well. A crimson snapdragon, for example, when crossed with a white one gives a *pink* F_1 hybrid. When selfed, this produces an F_2 in which one-fourth of

; are crimson (homozygous), one-half pink (heterozy-
l one-fourth white (homozygous), the one-to-two-to-one
:h we have just mentioned above. It is evident that
re *not a true Mendelian character at all, in the sense*
inherited and will segregate, but that it is merely the
. of two factors in a heterozygous condition.

ident Assortment.—When Mendel studied the inheri-
wo or more factors simultaneously he discovered the
nportant fact that segregation which takes place
he members of any one factor-pair *is quite independent*
hich takes place in any other, so that in the second
ı from the cross all sorts of recombinations, many
ite unlike those found in the original parents, may occur.
ısider a plant which is homozygous for purple flowers
or smooth seeds and which we may therefore represent
mula PP SS, to be crossed with a plant homozygous
flowers and also for rough seeds, WW RR. The for-
ıe F_1 hybrid offspring would of course be PW SR, and as
ed coat is dominant over rough, this plant would look
ırple-flowered, smooth-seeded parent. When gametes
:d by this plant, half of them carry the factor P
the factor W. But *it is clear that every sexual cell*
y within itself not only the factors for flower color but
: for seed surface and for all other plant characters,
.nd half of the gametes thus must carry the factor
' the factor R. Now we find that in any given sexual
purely a matter of chance as to whether the factor
: *flowers is associated with that for smooth seeds or*
for rough seeds. The particular combination of
ıich enters the F_1 plant from each parent (purple with
d white with rough, *in this case) has no effect* whatever
way in which they are associated in the gametes
by this plant. Their *assortment is independent.* Such
the F_1 hybrid in this example will therefore produce
; of gametes in equal numbers: P S; P R; W S, and
two such plants are crossed, there will be *sixteen*
ombinations among their sexual cells, for there will
.nds of pollen grains and four kinds of egg cells and
uite at random. Any one of these combinations is as
ɔccur as any other, and the sixteen types will thus
equally numerous. Since two of these characters are

dominant, the sixteen types will not all be visibly distinguishable, for the hybrids or heterozygous plants will resemble the pure dominants. The resulting F_2 generation is shown in Fig. 125. Our expectation in such a population is evidently that nine-

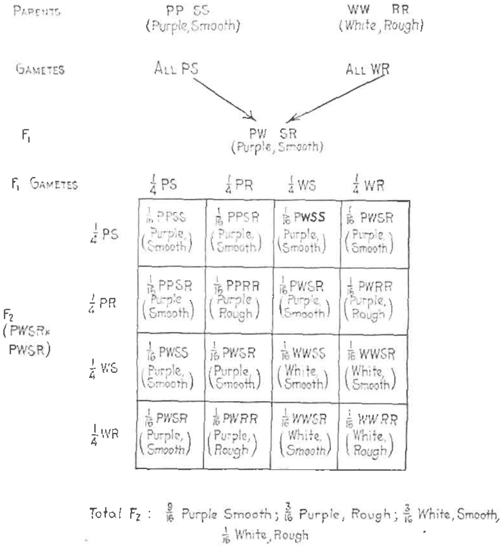


FIG. 125.—Diagram showing genotype (in letters) and appearance of parents, of F_1, and of F_2 in a cross between a purple-flowered, smooth-seeded pea and a white-flowered, rough-seeded one.

sixteenths will show both dominant characters, three-sixteenths one dominant and one recessive, three-sixteenths the other combination of dominant and recessive, and one-sixteenth, both recessive characters. The results of another such *dihybrid* cross are shown in Fig. 126. The method by which new combinations of characters are secured through hybridization is thus clear; but we must remember that many of the F_2 plants are

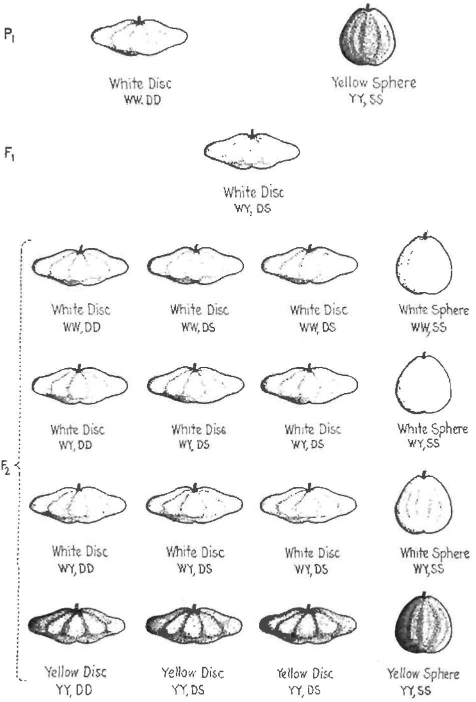


FIG. 126.—Mendel's law of inheritance, where two pairs of characters are involved. In summer squashes, disc shape in fruit is dominant over sphere shape and white color in fruit over yellow. A white disc crossed with a yellow sphere gives an F_1 generation all of which appear white disc. When inbred, this F_1 plant produces an F_2 generation which is about $\frac{9}{16}$ white disc, $\frac{3}{16}$ white sphere, $\frac{3}{16}$ yellow disc and $\frac{1}{16}$ yellow sphere. Many F_2 plants which look alike have very different genotypes. The appearance of the fruit and the genotype of the plant from which it came are given in each case.

heterozygous in one or both factor pairs and so will not breed true to their present appearance. The only F_2 individuals which will persist unchanged when inbred are those which are completely homozygous.

FIG. 127.—A mutation in tobacco. The Stewart Cuban variety, which produces an unusually large number of leaves per plant. (*From the Journal of Heredity*).

Such, in brief, are the essential features of "Mendelism". The intensive research of the past twenty years in the fields of both botany and zoölogy has shown that conditions in many

cases are not as simple as Mendel found them in garden peas. Some factors are "linked" together and do not display the independence of segregation which we have noted. Others depend for their expression not upon one but upon a whole series of independent factors. Others are influenced in appearance and inheritance by sex. Size characters in general (those of quantity as opposed to quality) rarely show simple Mendelian segregation at all but blend more or less completely and require for their investigation the use of measurements and statistical methods.

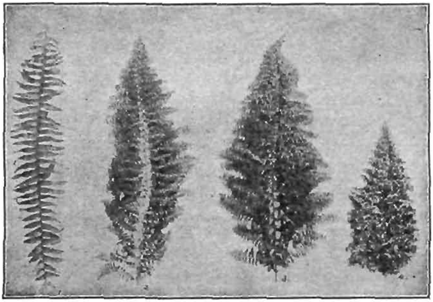


Fig. 128.—"Bud" sport or mutation, arising in a portion of the plant and not from seed. At extreme left a leaf of the original Boston fern, and, at right, leaves of three mutants which have arisen from it. (*Courtesy Brooklyn Botanic Garden*).

All of these cases, however, can be understood or explained by amplifying and interpreting Mendel's original law without at all destroying its fundamental principles, and it remains today as one of the most profound generalizations of biological science.

Mutation.—We have already spoken of the variations produced directly by differences in the environment to which the plant is subjected, *variations which apparently are never inherited.* It is now clear from our consideration of Mendelism that another and doubtless a very common cause of variation is the recombination of characters which follows the crossing of two different types or races; and these variations, being due to differences in the inherent genetic factors themselves, are clearly inheritable

FIG. 129.—Horticultural plants which have arisen from the wild cabbage. *A*, wild cliff-cabbage, *Brassica oleracea*, the probable ancestor of the group. *B*, broccoli. *C*, kale. *D*, kohl-rabi. *E*, brussels sprouts. *F*, cabbage. *G*, cauliflower. (*From Gager's "Fundamentals of Botany", P. Blakiston's Son and Co., Philadelphia*).

according to definite laws. *There is still a third type of variation*, often of importance in nature and in practical breeding, which we know as *mutation*. Frequently an individual clearly different from the rest will appear in a pure race, where there is apparently nothing in the ancestry which can explain its origin, and will breed true to this new type in succeeding generations (Fig. 127). The production of such a new and distinct type we call a mutation. Many "double-flowered" races of plants have arisen in this way, as have forms with cut leaves and a great variety of other characters. When the history of such a plant type can be traced, it is often found to begin with a single individual which arose by mutation from the normal race and has transmitted its characters to its descendants. In some cases a mutating individual is strikingly different from the normal form and is then often called a "sport". In others, the difference is so small that it can hardly be recognized. Many instances have also been found where the mutation appears in a single branch or portion of the plant rather than in a whole individual growing from seed (Fig. 128). All mutations agree, however, in coming without warning or evident cause and in being transmitted to offspring. By mutation have arisen some of our *important horticultural and crop plants (Fig. 129) such* as the kohl-rabi, the navel orange, the thornless cactus, the moss rose, the Shirley poppy, and others. We can understand and manipulate, to a certain extent, the variations due to environment and to hybridization, but mutations are as yet beyond our control. The best that the plant breeder can do is to watch for them closely and seize upon them when they appear.

The science of genetics is today one of the most intensively studied branches of biology and has not only yielded us valuable information as to the laws by which various characteristics are transmitted from parent to offspring, but through its identification of the chromosomes of the nucleus as the probable seat of genetic factors, it has even thrown light on the structure and behaviour of protoplasm itself.

QUESTIONS FOR THOUGHT AND DISCUSSION

577. What is the chief practical importance of discovering laws of inheritance?

578. In studies of inheritance in the summer squash it has been found that white fruit color is dominant over yellow, and that the differ-

ence between these two colors is due to a single factor. If a plant homozygous for white is crossed with a plant homozygous for yellow fruit color, what will be the appearance of the F_1 generation? of the F_2 generation derived by self fertilizing one of these F_1 plants? What proportion of the white-fruited F_2 plants will breed true if self-fertilized?

579. What will be the fruit color of the plants produced by crossing one of the F_1 individuals, mentioned in Question 578, with its yellow-fruited parent? with its white-fruited parent?

580. Let the factor for white fruit color in the squash be represented by W and that for yellow by Y. What kind of gametes, as far as their factors for fruit color are concerned, will be produced by plants having the following genotypes: WW, WY, YY?

581. What gametes will be produced by the plants involved in the four following crosses; and what will be the fruit color of the offspring from each cross:

WY × YY; WW × WY; YY × WW; WY × WY?

582. A white-fruited squash plant when crossed with a yellow-fruited one produces offspring about half of which are white and half yellow in fruit color. What are the genotypes of the parent plants?

583. If the white-fruited parent plant in the preceding question is self-fertilized, what will be the fruit color of its offspring?

584. If this same white-fruited parent is crossed with one of its white-fruited offspring mentioned in Question 582, what chance is there of obtaining from this cross a yellow-fruited plant?

585. Two white-fruited squash plants when crossed produce about three-fourths white and one-fourth yellow offspring. What are the genotypes of these two parents, as to fruit color? What will each produce if crossed with a yellow-fruited plant?

586. A cross between a white-fruited and a yellow-fruited squash plant produces offspring all of which have white fruits. If two of these F_1 plants are crossed together, what will be the fruit color of *their* offspring?

Note.—In Four-o'clock flowers, red flower color is incompletely dominant over white, the hybrids being pink-flowered.

587. If a red-flowered Four-o'clock plant is crossed with a white-flowered one, what will be the flower color of the F_1? of the F_2? of the F_1 crossed back on the red-flowered parent? of the F_1 crossed back on the white-flowered parent?

588. In Four-o'clock flowers, let R represent the factor for red flower color and W the factor for white. What will be the flower color of the offspring from the following four crosses, in which the parents' genotypes are given:

RW × RR; WW × RW; RR × WW; RW × RW?

589. If you wanted to produce Four-o'clock seed *all* of which would yield pink-flowered plants when sown, how would you do it?

590. In what respect is a character which behaves like flower color in Four-o'clocks easier to deal with in breeding work than one which behaves like fruit color in squashes?

Note.—In the inheritance of fruit shape in summer squash it has been found that the "disc" type is dominant over the "sphere" type (see Fig. 126).

591. In a cross between a squash plant homozygous for yellow fruit color and disc fruit shape and a plant homozygous for white fruit color and sphere fruit shape, what will be the color and shape of the fruit in the F_1? What will these be in the F_2 produced by crossing two of these F_1 plants together?

592. If one of the F_1 plants in the preceding question is crossed back onto its yellow disc parent, what will be the color and shape of fruit in their offspring? What will these be if the F_1 plant is crossed back onto its white sphere parent?

593. Let D represent the factor for disc fruit-shape and S the factor for sphere. What will be the color and shape of fruit in offspring of the following crosses:

WW SS × YY DD	WY DS × WY SS
WY DD × YY SS	WY DS × YY SS
WY DS × WY DD	WY DS × WY DS

Note.—In the following six questions, all of which deal with fruit color and shape in the summer squash, the appearance of parents and offspring is stated. Determine in each case the *genotypes of the parents*.

594. White disc crossed with yellow sphere gives one-half white disc and one-half white sphere.

595. White sphere crossed with white sphere gives three-fourths white sphere and one-fourth yellow sphere.

596. White disc crossed with yellow sphere gives one-fourth white disc, one-fourth white sphere, one-fourth yellow disc, and one-fourth yellow sphere.

597. White disc crossed with white sphere gives three-eighths white disc, three-eighths white sphere, one-eighth yellow disc and one-eighth yellow sphere.

598. Yellow disc crossed with white sphere gives all white discs.

599. White disc crossed with white disc gives 28 white disc plants, 9 white sphere plants, 10 yellow disc plants, and 3 yellow sphere plants.

600. A cross between a plant with white disc fruits and one with yellow sphere fruits gives 25 plants with white disc fruits, 26 with white sphere, 24 with yellow disc, and 25 with yellow sphere. If the white disc parent is self-fertilized, what proportion of its offspring will have yellow sphere fruits?

601. Explain how it can be that plants which look exactly alike may breed very differently.

602. Hybrid animals and plants notoriously fail to breed true. Why?

603. If a potato breeder desires to obtain a new variety of potatoes by selection from among a large number of plants, would you advise him to plant potato "seed" (pieces of the tuber) or real seed from the seed capsule, to provide plants from which he may select? Why?

604. Do you think that the characteristics of the fruits of an apple tree will be affected by the kind of pollen which fertilized the flowers? Explain.

REFERENCE PROBLEMS

96. Summarize briefly the life and work of Mendel and tell how his discoveries were finally brought to the attention of the world.

97. Give examples (aside from those mentioned in the text) of new plant varieties which have arisen as a result of hybridization; as a result of mutation.

98. State briefly why it is that the chromosomes, rather than any other part of the gametes, are believed to carry the hereditary factors.

99. What is a "Pure Line" of plants? Of what importance are Pure Lines in agricultural practice?

100. What is meant by "bud selection" in horticultural practice?

101. Give the derivation of the following terms and explain in what way each is appropriate:

Heredity	Segregation	Mutation
Allelomorph	Homozygous	Genotype

CHAPTER XII

EVOLUTION

Among all organisms which we can carefully watch and study, new variations are continually appearing and being inherited. This fact at once suggests that living things are not constant and changeless in their characteristics but that they may undergo a certain degree of permanent modification as the generations succeed each other. A glimpse at the remarkable development of our domestic plants and animals, since man first began to utilize them and to improve them by selection, shows the possibilities of change which exist among organisms. The difference between the small, sour prototype of the apple, for instance, and our modern large and delicious varieties is so great that we can hardly recognize the relationship between the two. In fact, many of our cultivated forms have progressed so far under human guidance that we do not know what their wild ancestors were.

Since the days of the Greeks, philosophers have often speculated as to the possibility that the whole organic world—plants, animals and man—has reached its present state through a gradual evolution from far simpler forms, perhaps ultimately from inorganic matter. It is only within the last century, however, that the subject of evolution has descended from these clouds of speculation and become a problem for scientific study. Little by little, evidence has been accumulating that progressive change has actually taken place, and that the plants and animals which we now know differ radically from their ancestors in past ages. As to just how this has been accomplished biologists are still far from agreed, but as to the *fact* of evolution there is now practically no doubt in the minds of scientific men. An insistence that every species was specially and suddenly created in exactly the form which it now displays has given way to the more profound conception of the world as the theatre of a slow but steady upward progress from lower to higher types of life.

Evidences for Evolution.—The lines of evidence on which the belief in evolution is based are various, and we shall briefly discuss a few of them.

Geological Evidence.—Probably of most importance is the existence of *fossils*, the actual remains or impressions left in the rocks by ancient plants and animals, caught and embedded in the sand or mud millions of years ago. As our knowledge of geology becomes greater, we find that fossils do not occur indiscriminately but that similar types appear in rock layers which we know, from their position, to be of about the same age. We

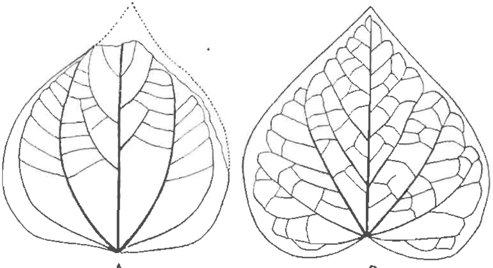


Fig. 130.—*A*, leaf of a fossil species of the Judas Tree (*Cercis*), from the Eocene of Tennessee. *B*, leaf of a living species, *Cercis canadensis*, now growing throughout the eastern United States. The two species are similar to each other but are clearly distinct. Our living species has probably been evolved from an ancestor much like the fossil one here shown. (*After Berry*).

are able to assign each rock layer, or stratum, to its particular level in the great series which records geological history from a very remote past to the present, and we find as we pass upward through this series, from the most ancient rocks to the most recent ones, that the fossil remains change progressively as we proceed; and that as we approach modern times, the prototypes of our familiar plants and animals begin to come into view (Fig. 130) until in recent deposits we find as fossils species which still exist. There are enormous gaps in this record but the advance of geological science is slowly filling them in, and even now we can catch a glimpse of the main scenes in the pageant of evolutionary progress. Among the members of the plant kingdom, we can witness the rise, luxuriance, and extinction of several great groups; we can trace the development of seed plants from lowly, fern-like forms, and we can recognize approximately the

point at which our modern flowering plants first appeared upon the earth. No other evidence for evolution is quite so convincing as are these tangible remains of extinct organisms.

Taxonomic Evidence.—The general character and classification of the plant and animal kingdoms also bears testimony that their present state is the result of descent, with progressive modification, from earlier types. A study of the external and internal structure of living things makes it clear that they are not haphazard and random in their characteristics, but that they fall into well-marked groups of similar forms, the members of which show definite resemblances to each other. All similar individuals we class together as a species. A number of species resemble one another so much, and are so different from anything else, that we place them together as a genus. A number of genera, in the same way, stand apart as a family. Families are united into orders, orders into classes, and so on. We can understand this grouping of similar species and their union into progressively larger aggregations if we regard the organic world as a huge "genealogical tree", its members related to one another—some nearly, some remotely—by ties of descent, the "twigs" representing species, which unite into larger and larger branches as we trace them back to the main trunk. These facts, which make the science of taxonomy possible, are unexplainable otherwise.

Morphological Evidence.—Equally significant are certain facts which morphology presents. Many organs exist today in a state evidently useless to the plant or animal possessing them and for which it is hard to account unless we look upon them as vestiges or remnants of structures which once had a use but have lost it during the course of evolution. Vestigial stamens, petals, sepals, stipules, and leaf blades, as well as various functionless internal structures, are of frequent occurrence in plants, and there are many similar instances in the animal kingdom. Their presence can be explained only if we assume that they once were well developed and functional but that evolutionary progress, which makes them necessary no longer, has resulted in their gradual degeneration.

Evidence from Geographical Distribution.—Impressive evidence in favor of evolution is presented by the facts of geographical distribution. Most plant species are not widely dispersed over the earth's surface, or even over that part of it in which conditions are well suited for their growth. The golden-rods, for

example, are practically confined to North America, the eucalypts to Australia, the tobaccos to the western hemisphere, and so on. We can explain such localized distribution only by assuming that these plants were evolved in the regions which they now inhabit, and have been confined there ever since by barriers of various sorts (Figs. 131, 132, and 133). The same phenomena occur

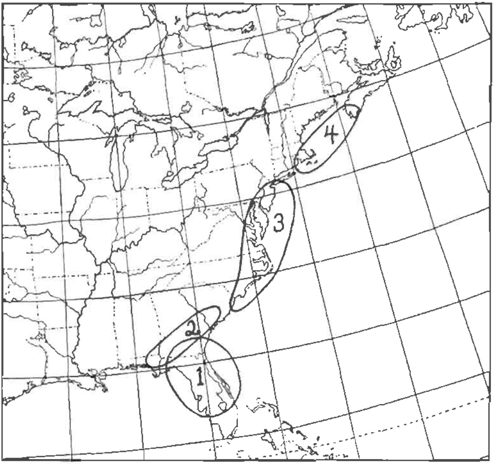


FIG. 131.—The distribution of four closely related species belonging to the same genus (*Sabatia*, section *Pleienta*). 1, *Sabatia decandra*. 2, *S. foliosa*. 3, *S. dodecandra*. 4, *S. Kennedyana*. These four very similar but readily distinguishable species have presumably all evolved from a common ancestor, which once grew on the coastal plain of southeastern North America. (*Data from M. L. Fernald*).

repeatedly throughout the animal kingdom, and it is certain that the great mass of facts which we now possess on the geographical distribution of organisms would be largely unexplainable if we did not believe that each species, genus, and family of plants and animals has had its place of origin and its own individual evolutionary history. The facts of distribution are meaningless on any other hypothesis.

Because of such facts as these, the scientific world has become convinced that evolutionary change has actually occurred and that the plants and animals with which we are now familiar are the most recent members of innumerable lines of descent, reaching

FIG. 132.—Three of the four species of *Sabatia* the distribution of which is mapped in Fig. 131. They are similar but quite distinct from one another. 1–3, *Sabatia Kennedyana;* 4 and 5, *S. dodecandra;* 6–8, *S. decandra.* (*From M. L. Fernald*).

backward for millions of years and embracing a multitude of ancestral forms entirely different from anything now alive.

An admission of the fact of evolution at once raises two grave questions, however; whence came the first living thing, the

original ancestor of all which have since evolved; and what has been the *cause* of this steady and long-continued evolutionary progress? The first question involves the origin of life, about which we must frankly admit that our ignorance is still complete.

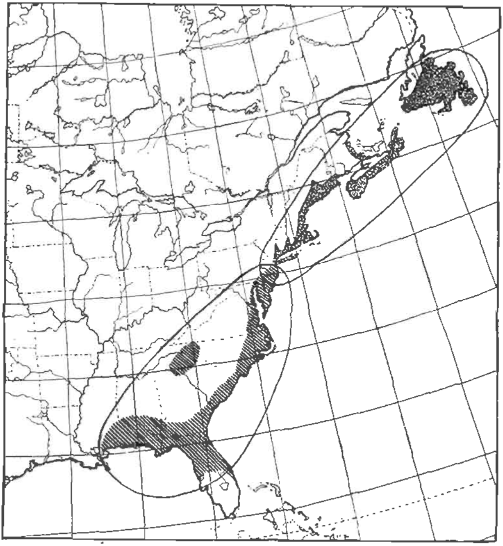


FIG. 133.—The distribution of *Gaylussacia dumosa* (lined) and its variety *Bigeloviana* (dotted). The species is characteristically southern, the variety northern. In New Jersey and adjacent Pennsylvania, where their ranges overlap, the variety merges into the species, but in the rest of its range it is quite distinct. Here we evidently have two groups of plants, within a single species, which occupy different regions and which have diverged from one another almost far enough to be regarded as two distinct species. (*Data from M. L. Fernald*).

The second, which relates to the cause and method of evolution, is more nearly solvable and has been the subject of intense interest and close study for more than a century. Indeed, it was our inability to explain why and how evolution might have taken

place that for so long prevented a general acceptance of the belief that it had really occurred at all. Although much progress has been made in this field of inquiry, we are still far from a complete and convincing solution of the many problems which the study of evolution has raised.

Lamarck's Theory.—The first modern theory which attempted to explain evolution was put forward by the great French biologist Lamarck about 1809. He was much impressed by the profound effect which the environment produces and noted many instances of its operation, such as the vigor and luxuriance of plants growing in rich soil as contrasted with their stunted growth where the soil is poor (Fig. 121). In the cases of several "amphibious" species he observed that leaves produced when the plant is growing under water are very different from those formed in the air (Fig. 81). He also observed the great structural changes which are brought about, in animals, by the use or the disuse of an organ. Lamarck believed that organisms possess the ability to react to their environment advantageously and to modify their structures and functions in such a way that success under a changing environment will be attained. He never questioned that all the variations which he noted were directly transmitted to offspring by heredity, and he thus pictured the races of plants and animals as being pushed along the evolutionary road by environmental forces.

Lamarck's explanation, although very attractive and plausible in certain respects, has never won wide acceptance. Biologists have as a rule not been willing to admit that an organism has any innate ability to guide its reactions into a favorable course. The theory has suffered still more from the absence, after intensive search, of any very conclusive evidence that "acquired" characters, such as those produced by the environment, are ever inherited. There are a few biologists today who believe that in certain of its features Lamarck's theory comes nearer to explaining the true method of evolution than any other yet suggested, but as a whole it receives little support.

Darwin's Theory. "Natural Selection."—The most notable attempt to solve the riddle of evolution is the theory of Natural Selection put forward in 1859 by Charles Darwin (Fig. 134) in "The Origin of Species", a book which has had a very great influence on all human thinking. The effect of this theory in rendering the whole process of evolution plausible and understandable

was the chief factor in convincing scientific men of the truth of the evolutionary theory in general; and whatever we may think today of the merits of some of Darwin's hypotheses, we recognize that the thoroughness of his scientific work and its revolutionary effect on all lines of biological thought entitle him to rank as the first great evolutionist.

Darwin based the theory of Natural Selection upon three main facts: *Variations and their inheritance; over-production of off-*

FIG. 134.—Charles Darwin, 1809–1882.

spring with the consequent "struggle for existence"; and the "survival of the fittest."

He was vividly impressed by the occurrence of variations in all animals and plants and studied them carefully, endeavoring to discover their causes. Like other scientific men of his day, Darwin did not clearly understand the mechanism and laws of inheritance. He believed, at least in his earlier work, that "acquired" characters may be transmitted to offspring, but this belief did not form the essential basis for his theory, as it did for that of Lamarck. The main fact which he emphasized was that variations in all directions are exceedingly abundant and that in many cases they are certainly transmitted by inheritance to the offspring.

The overproduction of progeny in plants and animals forms the next step in the theory. If all seeds which are produced were to

row and if all animal young were to mature, there would soon be o food or room for them on the earth's surface. Only a small action can possibly live to maturity. As a result, argues Darwin, here must necessarily be a terrific life-and-death competition, "struggle for existence", in which the few survive and the many erish.

Finally, those individuals in this struggle which possess any dvantage in structure or in function over their fellows, even this advantage is a very small one, will evidently have the best hance to succeed and survive. Of the manifold variations which lants and animals display, some will naturally be helpful nd some harmful, and those fortunate individuals which vary in he right direction will survive and transmit their advantageous haracters to their offspring. The others will perish and leave o descendants. Through this "survival of the fittest" the race ends to change steadily and to progress toward a type which is etter and better adapted to the conditions under which it is ving, and also to develop new types which can successfully ıvade new environments. Darwin named this process Natural election from analogy to the artificial selection long practiced y man with his domestic animals and plants, by which he has aused such great changes merely by selecting, for breeding ock or for seed production, those individuals which varied in uch a way as best to meet his requirements.

Objections to the Theory.—In support of his theory Darwin rought forth a wealth of evidence so convincing that it won very ide acceptance. As knowledge has advanced, however, various bjections to it have persistently been raised. Why is an advanageous character appearing in only one individual not lost, by swamping", in crosses between this individual and the rest of he population? Why do so many structures exist which are not vidently helpful in survival? Why are many species separated y differences so small that it is hard to believe that they are lifend-death differences? What causes the persistence and survival f early steps in the development of a structure, before it has ecome perfected and useful to the organism? If variations occur t random, as Darwin supposed, how does it happen that a complex nd highly coördinated structure could develop, since its producon would require innumerable variations of just the right degree, . just the right place, and at just the right time? Why have we

never been able to produce by artificial selection a group of individuals which could clearly be regarded as a new species?

These and other objections have been answered in whole or in part by Darwinians, but they are still of sufficient weight to convince most biologists that the theory just as Darwin left it cannot well be maintained today. No doubt natural selection eliminates vast numbers of obviously unfit individuals, but that it has been the most important factor in producing new forms, and thus in directing evolutionary progress, is now rather generally doubted.

De Vries's Theory.—*Another attempt to explain the cause and method of evolution has been made in recent years by the Dutch botanist de Vries, who believes that the small and almost imperceptible variations, regarded as most important by Darwin, are merely "fluctuations" around the normal type which have been produced by the environment and are therefore not inheritable.* The real variations which lead to evolutionary change, according to de Vries, are the *mutations.* These are permanent and inheritable, and are often large and conspicuous. The founder of the Mutation Theory thus looks upon organic nature as advancing by distinct and usually rather long steps rather than by an almost infinite number of small ones.

Although de Vries recognizes the importance of natural selection in evolution, his theory has certain advantages over that put forward by Darwin. If complex new characters and even new varieties and species can arise by one or even a few steps, the problem of the preservation of the early stages in the development of a useful structure is partly solved, and the existence side by side of distinct but very similar species is explained. The length of time necessary for evolution is also reduced. Many of the objections which have been urged against Darwin's theory, however, apply with equal force to that of de Vries, and although the latter has taught us the necessity of distinguishing sharply between inheritable and non-inheritable characters in evolution, it has not been accepted as a complete solution of the problem.

Orthogenesis.—These various theories lack a convincing explanation of the progressive appearance of new characters and their harmonious incorporation into the organism. The environment evidently cannot produce them, and it seems unlikely that mere random variations, whether large or small, would be any more successful. In view of all this, some biologists have

turned to the organism itself to discover the directive factor in the production of new forms. They believe that variation is not a random process but that in any given species, or succession of individuals, the variations tend always to be of a certain particular sort, characteristic of that species, and that the species consequently undergoes progressive change in a definite direction. The advocates of such a theory of *Orthogenesis*, or internally directed evolution, believe that evolutionary change is due to the unfolding of certain tendencies in the protoplasm of the plant or animal, and is not forced upon the organism from without. They recognize the importance of natural selection in eliminating the radically unfit, but believe this agency quite unable to create anything new or to produce the organic world as we know it today.

It must be admitted that as yet we do not fully understand the manner in which evolution has taken place and the factors which have been responsible for it. In the past there has been perhaps too much unsupported speculation on the problem and too little pursuit of facts. The present intensive experimental study of heredity, physiology, cytology and morphogenesis will, it is to be hoped, provide us with a fund of information wherewith we may attack this central problem of biology.

QUESTIONS FOR THOUGHT AND DISCUSSION

605. Why is it that we do not regard new strains of corn, apples, and similar plants as new *species?*

606. Why does the record of plant and animal evolution given us by fossils have such large gaps in it?

607. What types of plants and animals would be most likely to be preserved as fossils?

608. Characters which are apparently of the least functional importance to the plant are often most constant throughout large plant groups and therefore very valuable in plant classification. Explain.

609. Most of the members of the Figwort family have four stamens in the flower, but there is often the rudiment of a fifth. The families most nearly related to the Figworts have five stamens. What can you infer from these facts as to the evolution of the flower in the Figworts?

610. The plant population of an isolated island or island group in the ocean (such as the Hawaiian Islands) is composed very largely of species

which are found nowhere in the world except on that particular island or island group. Explain.

611. The potato, tomato, tobacco and various other agricultural plants which are now grown in Europe were introduced there from America after the discovery of the New World. What can you conclude as to their evolutionary history?

612. *Torreya*, a genus of coniferous trees, is represented by two species in China, one in California, and another in the southeastern United States, but is found nowhere else in the world. What conclusions can you draw from these facts as to the past history of this genus?

613. In the Galapagos islands very many of the plant *species* are confined to this group of islands, but most of the *genera* are the same as those found on the adjacent coast of South America. In Hawaii, the species are not only distinctive of the islands but many of the genera also are found nowhere else. Which of these two island groups on the basis of these facts, do you believe has been isolated the longer and the more effectively? Why?

614. Plants living in arid or desert regions usually have small and leathery leaves and deep root systems, in contrast to plants living in regions of more abundant moisture. How would Lamarck explain this? How would Darwin?

615. Most plant species which are very common belong to genera which are larger than the average in number of species. Explain.

616. Darwin noted that species belonging to large genera were usually more variable than species belonging to small genera. Explain.

617. Which species is apt to be more successful, do you think, a relatively variable one or a relatively constant one? Why?

618. Which do you believe would change more rapidly in evolution, a species which is always cross-fertilized or one which is always self-fertilized? Why?

619. State at least five advantages which one plant species might have over another which would make it more widespread and successful.

620. Give an example of a physical barrier to plant distribution; of a "biological" barrier.

621. Is competition generally keener between two individuals of the same species or between two individuals belonging to different species? Explain.

622. Is competition apt to be keener between closely related or between distantly related species? Why?

623. In most cases, individual plants may be assigned to very definite species, and between these species transitional individuals are rarely or never found. If species have been developed through a gradual evolution, why are such transitional forms absent?

624. What characteristics must a successful weed possess?

625. A weed introduced into a new region often becomes more widespread and successful there than in its native land. Explain.

626. The chestnut bark fungus, introduced some years ago into the United States, has exterminated all the native American chestnut trees over wide areas. In China, its native home, the species of chestnut are almost immune to its attack. How do you explain this difference between American and Chinese chestnut trees?

627. Some species of plants produce comparatively few seeds but are just as successful as others which produce a great many more. Explain.

628. During the glacial invasion, the vegetation of the northern United States was obliged to migrate hundreds of miles south of its original range, and as the ice retreated it migrated northward again. Doubtless many plant species were exterminated during these changes. What characteristics should a plant species possess to survive such a migration successfully?

629. Name at least five different causes which might lead to the extinction of a plant species.

630. Why is it that all ancient and primitive types of plants have not been exterminated by the competition of those which have been more recently evolved?

631. A highly specialized and complex plant species is sometimes far less successful than one which is much simpler and more ancient in type. Compare, for example, our common bracken fern, which thrives over almost all the world, with many of our orchids, which are often rare and have very limited ranges. How do you explain this?

632. In the evolutionary history of many groups of animals and plants, as shown by their fossils, there is a gradual change from the simple and primitive members to those which are progressively more and more complex and abundant; but when a very high degree of specialization has arrived, the group suddenly becomes extinct. How do you explain this?

633. Primitive and ancient types of animals and plants are most common in comparatively isolated regions. Why?

634. Do you think that evolutionary change would take place more rapidly in a region freely exposed to immigration from without, or in a comparatively isolated region? Why?

635. The great land mass of Europe and Asia is believed to have been the center of evolution for many types of animals and plants now found in other parts of the world. Why?

636. Are the most widely spread plant species the oldest, do you think? Explain.

637. In consequence of the "struggle for existence" and the "survival of the fittest," why is it that in a given locality one species does not exterminate all the others and compose the entire vegetation?

638. Name a few of the changes in the natural vegetation of the world which have been brought about by civilization.

REFERENCE PROBLEMS

102. Give an example of a new variety of cultivated plant which has recently been developed by plant breeders.

103. About how long do geologists estimate that life has existed on the earth?

104. What are the great geological periods into which the ancient history of the earth has been divided by geologists?

105. Summarize the life and work of Lamarck and state his important contributions to botany.

106. Summarize the life and work of de Vries and state his important contributions to botany.

107. Give the derivation of the following terms and explain in what way each is appropriate:

Evolution	Fossil	Orthogenesis

CHAPTER XIII

THE PLANT KINGDOM

Through a period reaching back into the past for millions of years, such a long time that the entire span covered by human history seems almost negligible beside it, the evolutionary advance of the plant kingdom has gone slowly but steadily onward. We may still be uncertain as to the causes which lie behind this tremendous progressive movement, but its results are manifest in the scores of thousands of plant species with which the earth is covered today. Those of us who are familiar with the vegetation of the temperate zone, thriving and vigorous though this may be, can have little idea of the luxuriance and variety of plant life exhibited in tropical and subtropical regions. In New England there are about 4,000 species of seed plants, but probably 50,000 occur in Brazil, and in the whole world there have already been described a vast array of almost 250,000 species. Nor is our knowledge by any means complete. Although for the past three hundred years botanical exploration has been active in all parts of the globe, the discovery of new species is still constantly being reported. It is the seed plants which constitute the dominant and conspicuous part of this multitudinous vegetation, and in the present volume we have confined our attention almost exclusively to them, but we should remember that the plant kingdom includes a host of lower and simpler members. Of the ferns and their allies we now know more than 4,500 species, and in many parts of the earth they are an important element in the plant population. Of the liverworts and mosses there are some 16,000 species, and these are far exceeded by still lower forms, the fungi with 60,000 species and the algae with 20,000. In all these groups, exploration and critical study are yearly adding many new forms and it is safe to estimate that, were our knowledge complete, we should be able to recognize not less than 300,000 species of plants. The day has passed when any one botanist can hope to become familiar with more than a small portion of the flora of the globe.

That record of remote events which has survived to our day in the form of fossil plants makes it clear that the panorama of the earth's vegetation has repeatedly changed, that group after group has arisen, flourished and disappeared, and that thousands of species have evolved only to become extinct. Plants of today are the product of a long period of evolutionary development, and to understand the vegetable kingdom and its relationships we must therefore know something of the main events in its history.

Plants and Animals.—Plants and animals constitute the two great branches of the organic world. In their lowest representatives they are often hard to distinguish from one another, and certain simple forms exist which clearly combine the characters of both kingdoms. The earliest of living things would perhaps have been difficult for us to classify, but as evolution progressed, animals and plants became clearly distinguishable through the development among their members of certain characteristic traits. The animal tends to be motile, to ingest its food through a mouth, and to depend on other organisms as sources of food supply; the plant, to be stationary, to absorb its nutrient materials in solution over a considerable area of the body, and (except in the fungi and a few others) to manufacture its own food from simple inorganic substances. Many other differences in structure and function are associated with these fundamental ones.

Forward Steps in Plant Evolution.—During the divergent history of the two great groups, certain notable events took place in each with which the student of biology should become familiar. Before discussing the classification of the plant kingdom which follows in the succeeding chapters, we shall therefore consider briefly a few of the important steps which have marked its development.

The causes which led to the appearance on our earth of the first living things, and the characteristics which these primitive organisms displayed, are buried so deeply in antiquity that we shall probably never discover them. There is good reason to believe, however, that among the earliest of all plants, thriving in the warm primeval seas, were simple, single-celled forms which multiplied by simple division or *fission*, possessed chlorophyll or a similar substance, and in their general characters were not greatly unlike some of the simplest of our living algae. For ages they doubtless were the only vegetable life on the globe.

1. The Multicellular Plant.—The first great forward step which, like all first steps, was probably a long time in being accomplished, consisted of *the union of these simple cells into colonies* (Fig. 135). The two daughter-cells formed at a division remained attached to one another instead of separating, and thus arose small cell-groups or aggregations such as we still may see among the lowest algae. The individual cells forming these *groups might cohere variously—in* spherical masses, in threads, or in sheets. Through a still more intimate union between their members these cell colonies gradually developed into definite *multicellular plants*, various in size and shape and probably much like some of the simpler seaweeds of today. The

FIG. 135.

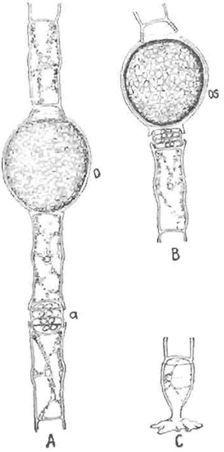


FIG. 136.

FIG. 135.—The beginnings of a multicellular plant. A simple alga, *Pleurococcus*, in which the plant body is commonly a single cell, but in which the daughter cells following cell division may remain united in very simple colonies.

FIG. 136.—The beginnings of differentiation. A thread-like or filamentous alga, *Oedogonium*, in which the cells are no longer all alike but have begun to be differentiated. One is modified as a *holdfast* (*C*), others as male sexual organs (*a*) and others as female sexual organs (*o*).

way was thus opened for the production of those very large and complex plant bodies with which we are most familiar.

2. Differentiation.—The evolution of the many-celled plant was soon followed by another and equally important advance, the beginning of *differentiation* (Fig. 136). The primitive single cell performed all the functions which we now associate with the entire plant, such as absorption, photosynthesis, and reproduction. Soon after the multicellular individual had arisen, how-

ever, there began to appear within it the same tendency which manifests itself in the evolution of a human society, the "division of labor". Instead of the primitive condition in which *all* the individual cells carry on *all* the functions, certain cells became specialists, some of them gradually assuming the performance of one function and some of another, and acquiring through this specialization a more or less conspicuous modification in structure. The first activity of plants to be thus localized was probably *reproduction*. Instead of a condition where every cell divided and gave rise to new individuals, certain ones were set apart to produce specialized reproductive cells or *spores*, provided with means of locomotion or other facilities which made them particularly well adapted to establish a multitude of new and widely scattered plants. This process of differentiation has steadily progressed during the evolution of the plant kingdom and has resulted in the marvelously complex individuals which we have studied among the seed plants. Here the various functions have *organs* devoted to their performance and in these the cells, far from being uniform, are grouped in definite and highly specialized *tissues*, each of which plays its particular part in the life of the whole. Differentiation has made possible the existence of the higher plants, and is one aspect of that phenomenon of *organization* or *regulation* to which we have so often called attention.

3. Sexual Reproduction.—Another important step in the history of the plant kingdom involved the method by which reproduction took place. In the earliest plants, this process was accomplished merely by a division of the cell into two. In forms a little more advanced, special cells became differentiated, each of which was able to produce a new plant. Following this stage, the type of reproduction which we know as *sexual* probably made its appearance. The essential feature of this method is the *fusion* of two cells into one and the subsequent development therefrom of a new individual (Fig. 137). The cells which thus unite are called sexual cells or *gametes*, and the product of their union, the *zygote*. In early plants, the gametes were probably nothing more than the ordinary non-sexual reproductive cells which had assumed this additional function; and in some of the algae today we find cells of this sort, which may reproduce the plant either sexually or asexually. Soon the gametes became clearly distinct, however, and asexual reproduction was often

given up, or resorted to only under special conditions. The sexual cells themselves became further differentiated into two sorts—small, active *male* gametes or *sperms* and larger, nonmotile *female* gametes or *eggs*, a condition which now accompanies sexuality so commonly that instances of equal gametes are com-

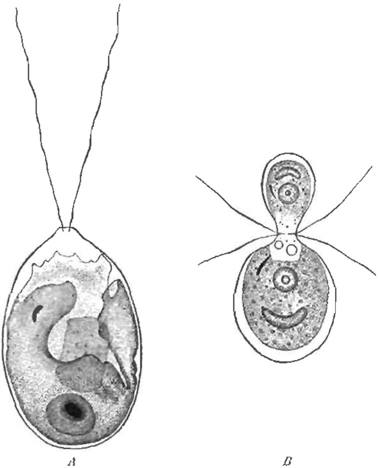


FIG. 137.—The beginnings of sexuality. A very simple alga, *Chlamydomonas*, (*A*) in which two cells may be differentiated as gametes and unite with each other. From their union a group of new individuals arises. In the case of fertilization here illustrated (*B*) the gametes are slightly different in size, foreshadowing the development of *male* and *female* gametes. (*A after G. S. Torrey*).

paratively rare. The causes which led to the development of sexual reproduction are unknown, but the process is so nearly universal, not only among plants but throughout the animal kingdom, that we are forced to believe it must have some special significance. There is evidence that sexual fusion results in increased vigor, particularly when the two gametes come from different individuals; but we also know many plants which may reproduce indefinitely by various asexual processes without evident loss in vitality. However that may be, a considerable

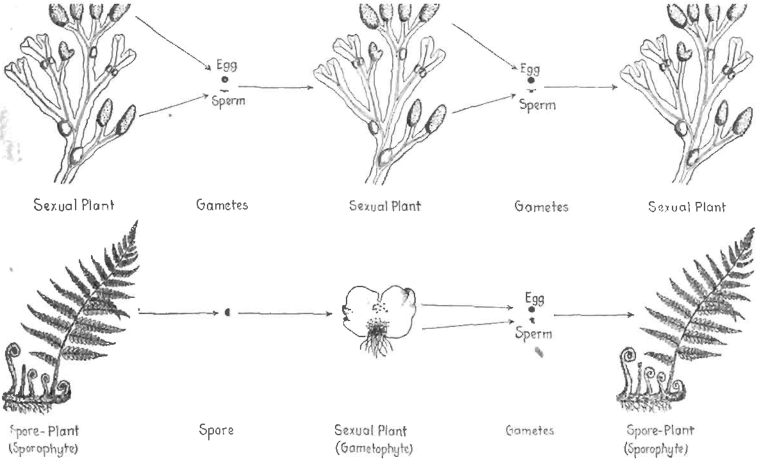


FIG. 138.—The essential features of the Alternation of Generations, brought out by contrasting a plant which displays it with one which does not. Above, the rock-weed (*Fucus*). The plant produces gametes, fertilization occurs, and from the fertilized egg a new plant develops directly. Below, a fern. *Here there are two independent plant types which alternate with one another. The fern* proper (spore-plant or *sporophyte*) is sexless and produces non-sexual *spores*. The spore germinates into a sexual plant or *gametophyte* on which sexual organs are borne. These produce gametes, and from the fertilized egg develops a new sporophyte.

proportion of the activities of plants seems to be devoted to the successful accomplishment of the sexual process.

4. **Alternation of Generations.**—The three steps in plant evolution which we have mentioned—the appearance of the multicellular individual, of functional and structural differentiation, and of sexual reproduction—occurred also among animals. The fourth belongs exclusively to the plant kingdom. It is the evolution of that remarkable double life-cycle which we know as the "alternation of generations" (Fig. 138), a process simple enough in its underlying principle and in its expression among the lower plants, but which in the higher groups leads to such complexities than an understanding of the process of reproduction is more difficult in the vegetable kingdom than among animals.

A. *In Thallophytes.*—In most members of that great and primitive group the Thallophytes, which include the algae and the fungi and which is the lowest of the four main divisions of the plant kingdom, a fertilized egg gives rise directly to a single new individual, just as is the case among animals. Beginning rather obscurely among some of the higher Thallophytes and reaching its full expression first in the liverworts and mosses, we find a modification of this simple and direct method. The fertilized egg, instead of producing a new plant like the parent, divides into a group of cells which separate and are liberated as non-sexual spores. Each spore may now give rise to a new plant. *In this way a single sexual union produces a whole group of new plants instead of one;* and it is this advantage, seized upon and perfected by early members of the plant kingdom, which probably led to the characteristic "alternating" systems of reproduction in all plants above the Thallophytes—a fertilized egg producing a group of spores, each of which grows into a sexual plant, in which fertilization again takes place.

B. *In Bryophytes.*—Such a simple condition as this, however, was evidently soon outgrown and now occurs among only a few lowly forms. The rapidly enlarging group of cells which had their origin from the fertilized egg soon began to produce something more than a mass of spores. The outermost cells became differentiated into a protecting wall, and the spore-case or

sporangium was thus formed. The cells at the base of this structure further developed into a support or stalk which lengthened and carried the sporangium up into the air, whence the spores might readily be dispersed. This general situation, where the sexual plant produces a spore-case borne on a well-developed stalk, is characteristic of the second main division of the plant kingdom, the Bryophytes, which include the liverworts and the mosses.

C. *In Pteridophytes.*—The next stage in the development of the "alternating" life cycle involved a radical change, and since the plants in which this change took place have long since perished and have left no descendants to our day, we can only surmise as to what actually happened. The sporangium and its related structures underwent a remarkable transformation, developing chlorophyll-bearing leaves which manufactured its food supply, and finally sending forth roots into the soil and thus establishing a new and entirely independent individual. Instead of producing but one sporangium, this now gave rise to many. In short, a spore-bearing, non-sexual plant, the *sporophyte*, had been evolved, entirely distinct from, and independent of, the older gamete-bearing, sexual plant, which is known as the *gametophyte.** This is the situation as we meet it in the third great division of the plant kingdom, the Pteridophytes, which include the ferns, club mosses, horse-tails, and their allies (Fig. 138). Here the dominant, conspicuous plant, with which we are most familiar, is the sporophyte. It produces thousands of sporangia and perhaps millions of spores, but sexual organs and gametes are entirely absent from it. It has evolved from the primitive moss sporangium and its associated organs. The gametophyte, however—the structure which corresponds to the moss plant—is small, inconspicuous and often hard to discover. It possesses no true roots or leaves but bears the all-important sexual cells. Here the fusion between gametes takes place, and from a fertilized egg in one of these inconspicuous gametophytes is developed a young spore-bearing plant. This soon develops leaves and roots and becomes independent of the parent gametophyte, which then withers away. Each of the many spores borne by

* The terms *sporophyte* and *gametophyte* are also used among Bryophytes, the former being applied to the spore-case and its related structures and the latter to the plant itself.

this spore-plant will germinate and grow (if conditions are favorable) and will develop in turn into a new gamete-plant, which will produce gametes and effect fertilization as before. In such a life-cycle as this, there are two distinct, independent and alternating plant types or "generations," each always producing the other. It was a study of conditions in these Pteridophytes which led to the term "alternation of generations", and which caused us to realize the significance of the peculiar methods of reproduction found in both the mosses and the seed plants.

Another notable distinction between gametophyte and sporophyte lies in the number of chromosomes found in their cells. In the former this number is only *half* as great as in the latter. The gametophyte really begins at the "reduction division" (p. 187), which occurs in one of the cell divisions preceding the formation of the spores, and ends with the union of the gametes in fertilization, which restores the double chromosome number and begins the sporophyte.

D. *In Spermatophytes.*—Finally, in the fourth and highest division of the plant kingdom, the Spermatophytes or seed plants, the alternation of generations has reached a still further stage of specialization. Here the gametophyte, instead of being an independent structure, now remains attached to and dependent upon the sporophyte. Furthermore there are now two kinds of spores, the *microspores* (essentially what we know as pollen grains) which develop into much reduced male gametophytes, producing only male gametes; and the *megaspores*, borne in the ovules, and developing there into female gametophytes, producing only egg cells.* At maturity, the male gamete comes down the pollen tube and fertilizes the egg in an ovule. From this union the young sporophyte develops as the embryo of the seed, and will in turn grow into a plant producing thousands of spores. In the seed plants, both gametophytes are much reduced in size and have so lost their primitive character that it was long before they were recognized as gametophytes at all.

In the history of the plant kingdom we thus pass from plants which are, like animals, entirely gamete-bearing (in the Thallo-

* Microspores and megaspores are differentiated in a few of the higher Pteridophytes, which we shall later describe. No seeds are developed among these plants, however.

phytes) to those in which the gamete-plant alternates with a *small, dependent, spore-bearing structure, the primitive sporophyte* (in the Bryophytes); thence to forms where sporophyte and gametophyte are both independent plants but where the former is now the large and conspicuous member (in the Pteridophytes); and finally to those in which the gametophyte is the dependent and subordinate generation, and where the only plant which we know as such is the spore-plant (in the Spermatophytes). A knowledge of this progressive development will not only aid us in understanding the process of reproduction in plants but is *perhaps the best approach by which we can gain a clear conception* of some of the important distinctions between the four great divisions of the plant kingdom.

5. The Invasion of the Land.—The fifth great forward step in plant history was the evolution of a type able to grow in the air rather than in the water, and which thus made possible an invasion of the dry land and the establishment there of a real terrestrial vegetation. We have said that plant life probably began in the sea. Here also doubtless took place the first great steps in the evolution of the vegetable kingdom; and although the seas teemed with life, the land masses of our earth were for a very long period of time barren wastes, or at best covered in their damper spots only with a scum of algae. This great area was freely open to whatever plant pioneer should be able to master the difficulties of such an environment.

Difficulties of Terrestrial Life.—These difficulties were many and formidable. First and most serious among them was the problem of maintaining, in such dry surroundings, a sufficient supply of water for protoplasmic activity. We have discussed in an earlier chapter the supreme importance of water in the life of plants, and have shown how indispensible it is in all physiological processes. When the whole plant body is immersed in water, as is the case in primitive and lowly forms, an ample supply of this substance is always at hand. If a plant part is lifted up into the air, however, it is at once exposed to the danger of water-loss through evaporation, which will soon result in death. This danger of drought has always faced plants which grow upon the land. If a plant is to succeed in such an arid environment it must be able both to absorb water in large amounts and to hinder the loss of water from its tissues by evaporation. Since the soil

provides the only source of water available to a land plant, it is evident that roots or root-like structures must be developed to *penetrate the soil and absorb water therefrom abundantly.* A successful accomplishment of photosynthesis requires a large *area of chlorophyll exposed to sunlight, and hence broad sheets* of chlorophyll-bearing tissue, "waterproofed" to prevent undue *evaporation, must also be evolved. These sheets we call leaves.* The leaves cannot be too close together without depriving one another of the necessary light, and they must therefore be spread out and separated in some way on an axis or *stem.* The region where water is constantly needed to replace water loss may thus be far distant from the region where it is absorbed, and a well developed conducting system to carry water from root to leaf must therefore be differentiated in the tissues of the stem.

Aside from the difficulty of maintaining a sufficient supply of water, the land plant also faces problems of a mechanical nature. Owing to the buoyancy of water, a plant growing submersed therein needs little or no mechanical support. If it grows in the air, however, there is much weight to be carried and a heavy strain to be borne by the stem, especially in its lower portions. An extensive development of thick-walled skeletal and supporting tissue is thus necessary, especially in the stem, if the plant is to be kept firm and erect.

In order to be able to thrive on land a plant must therefore possess successfully functioning roots and leaves, and a stem able to serve as an efficient means of conduction and support. Such structures are unknown in the Thallophytes, and these plants have therefore never been able to invade the dry land and to produce a true terrestrial vegetation, although they often thrive in moist situations on land and survive long periods of dryness in a dormant state. The first group to emerge from the water and develop land-inhabiting forms were probably the Bryophytes or plants like them, which may perhaps be called the "amphibians" of the plant world. They are best developed in moist places, though a few are aquatic and many grow in situations which are dry much of the time. Even in the most highly developed mosses, however, the root system is very weak and consists only of delicate thread-like *rhizoids;* the leaves are small and very thin, and the stems weak and with little or no development of supporting and conducting tissue. The mosses,

therefore, do not grow more than a few centimeters high and have never succeeded in producing a strong and vigorous land vegetation.

Success of the Pteridophytes.—It is a different matter with the Pteridophytes, however. The dominant generation here, as we have seen, is the sporophyte; and this new plant type, at least in all the forms which have survived to the present day, seems to be particularly well adapted to terrestrial life. Here for the first time we meet with true roots—large, vigorous, much-branched structures, each terminating in a mass of roots hairs and well suited for rapid absorption and strong anchorage. The leaf, instead of being a small and thin plate of tissue, is large and relatively thick. It has a well-developed mesophyll of thin-walled cells and is provided with abundant air spaces, the whole structure being covered by a stout epidermis to cut down evaporation. The necessary passage of gases between the outer air and the internal tissues of the leaf takes place through characteristic pores or stomata. The stem reaches a structural complexity nowhere exceeded among plants, the tissues for support and conduction being particularly well developed. The evolution of the true root, the true leaf, the stoma, and the highly differentiated stem made it possible for Pteridophytes to produce the vigorous and abundant land vegetation which covered the earth in ancient times; and from this group have come the seed plants, which form the bulk of the terrestrial vegetation of today.

There is evidently a wide step between the mosses on the one side and the ferns on the other. Transitional forms which must have existed between these two have entirely disappeared, and we can only guess what the plants were like which connected the Bryophytes and the Pteridophytes, and what were the first steps in the evolution of the well-developed land-inhabiting sporophytes which are so conspicuous today. This successful invasion of the dry land stands out as one of the most important and dramatic events in the history of the plant kingdom.

6. The Evolution of the Seed.—The last great progressive movement which we shall consider is the comparatively recent one which carried the process of reproduction to a still higher degree of efficiency and resulted in the development of that most perfect of reproductive structures, the *seed.*

The production of seeds is the distinctive feature of the

Spermatophytes or seed plants, which are now the most successful of all the higher plant types. The spore has several obvious disadvantages as a means of producing a new plant, owing to its minute size. Among the lower plants these difficulties are partially overcome by the production of spores in huge quantities, but the system of independent, free-living gametophytes, developed from single-celled spores, is subject to many difficulties at best. In the seed plants, as in a few of the most advanced Pteridophytes, there are (as we have previously noted) two kinds of spores—microspores and megaspores—which produce male and female gametophytes, respectively. The happy innovation introduced by these highest plants, however, was to retain the single megaspore within the sporangium, intimately attached to the mother plant, where it germinates into a much reduced female gametophyte. This whole structure, with the addition of a coat or *integument*, is the *ovule*. Only a few ovules, in comparison with the great number of spores formerly produced, are borne by the plant. The microspores (pollen-grains) are still liberated into the air in great numbers, just as among lower plants, but instead of falling on the ground and germinating there, they are carried to the ovule or near it, where each produces two male gametes, one of which may fertilize an egg.

Not only have the seed plants abolished the delicate, free-living gametophytes, with all the consequent dangers and difficulties in the process of reproduction, but they have also established a much more successful method for insuring the growth of the young plant. The fertilized egg grows at once into the embryo, which draws the materials for its development directly and abundantly from the mother plant, and is thus relieved of the necessity of producing them by its own activity. About the embryo is deposited this supply of concentrated food in the form of endosperm. The growth of the embryo ceases after a young root and one or two primitive leaves have been formed; and embryo and endosperm, tightly enclosed in the integument of the ovule which has now become very tough and strong, is known as the *seed*. This becomes detached from the parent plant and may remain in a dormant condition for a long time, sometimes many years; but on the occurrence of favorable conditions it will germinate and the embryo within it will begin to grow, bursting its shell, absorbing the stored food, sending forth roots

and leaves, and rapidly developing into a new plant. The many advantages of reproduction by seeds over the old method of wind-blown spores and independent gametophytes are obvious, *and it is easy to see why the seed-plants have become so dominant and successful.*

Plant Classification.—As the result of these slow, progressive changes, which have been working themselves out gradually through millions of years, we see around us the plant kingdom of today, occupying almost every corner of surface on land and sea and consisting of an enormous variety of species. The task of the science of taxonomy is not merely to list and describe these species, but to *classify* this great array by distinguishing and bringing together groups of species which resemble each other, thus reducing our knowledge of the plant kingdom to that orderly arrangement which is the aim of all science. Ever since the dawn of botanical study, men have been endeavoring to construct such a classification and the results are very diverse. One of the earliest attempts used the resemblance in growth-habit as a basis of classification and divided plants into three groups,—trees, shrubs, and herbs. As botanists learned more about the vegetable kingdom, such crude systems were seen to be wholly inadequate, and resemblances of a much more deeply-seated kind began to be noted, based on a larger number of characteristics. Thus the conception of plant "families" began to take form, and the Rose family, the Carrot family, the Legume family, and many others were distinguished and described. There were still wide differences of opinion as to what the groups should be and how they should be subdivided, and there were almost as many "systems" as botanists. Indeed, on the theory which assumed that all plants had been created at the same time, it was difficult to see why these well-marked groups of similar species should exist at all, and there was really no rational foundation for any system of classification.

The establishment of the theory of evolution in the latter part of the nineteenth century, however, threw a flood of light on the whole problem, for it showed that resemblance among members of a plant group was not an arbitrary or chance one but was due to the fact that all the members *had descended from a common ancestor.* Classification became thereupon a definite effort to work out a genealogy or "family tree" for the plant kingdom, or for a given group within it, similar in its type to that which we might construct

for any family (Fig. 139). The problem confronting the taxonomist today, therefore, is not the recognition of certain rather vague "affinities" between plants, but simply the determination of what might be called their "blood relationships"; and during the past fifty years particular emphasis has been placed on the

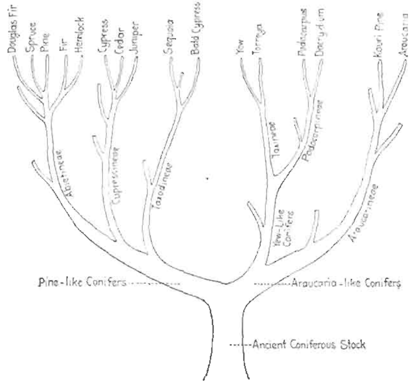


FIG. 139.—A suggested "family tree" for the Conifers. According to this hypothesis, the ancient coniferous stock long ago divided into two groups, each of which has given rise to three modern families or sub-families. Two of these (the Taxineae and Podocarpineae) are more closely related to each other than they are to the other families. Within the Abietineae there are evidently two distinct groups of genera. The branch stumps represent extinct groups. The twigs are genera of coniferous trees which are living today. Such a diagram as this makes *it possible to show graphically the inter-relationships between the various* members of a group of plants.

science of Phylogeny, which endeavors, through a study of fossil *history, comparative anatomy, and other sources, to trace out* the complicated problem of ancestry and descent throughout the whole plant kingdom. The findings of this science are of great importance in providing a basis for classification. While there are still differences of opinion as to facts, everyone is agreed that the ideal to be attained is a system of classification which is truly a "natural" one, or based on descent. As our knowledge of the evolutionary history of the plant kingdom becomes more

complete, our systems of classification will grow more accurate and useful.

Groups within Groups.—Plant classification is far more complex, however, than a mere segregation of individuals into a series of distinct groups, for each group is further subdivided into smaller ones and each of these, in turn, into others still

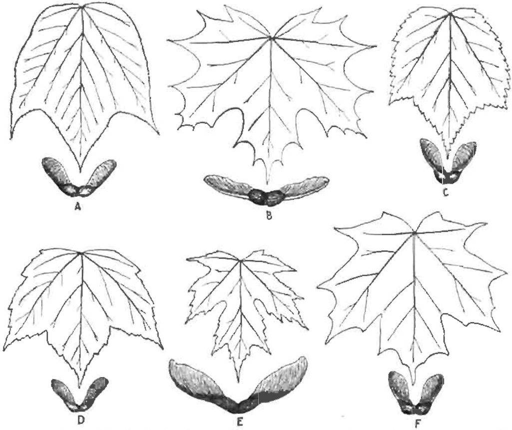


FIG. 140.—*Species* belonging to the same *genus*. Six species of maple (*Acer*) represented by leaf and fruit. Each species is readily distinguishable from the rest by its own individual peculiarities, but in all the species the fundamental characteristics of the maple genus are evident. *A, Acer Pennsylvanicum. B, A. platanoides. C, A. spicatum. D, A. rubrum. E, A. saccharinum. F, A. saccharum.*

smaller. This system of "groups within groups" is familiar in methods of classifying all sorts of objects. An army, for example, has a definite system of organization or classification, whereby it is separated into a series of large groups, or divisions. Each division, in turn, is made up of brigades; each brigade, of regiments; each regiment, of battalions; each battalion, of companies; each company, of platoons; and each platoon, of squads. In this way every soldier occupies a definite and particular place

in the organization. In the taxonomy of the plant kingdom a somewhat similar series of groups within groups has been recognized and its parts named, precisely as in a military organization. The most important of these groups are the *species*, *genus*, *family*, *order*, *class* and *division*, although additional ones are often employed. Thus all the individuals which are like one another are grouped together and constitute a *species*, of which we may take the Dog Rose as an example. This species is clearly very similar to a large number of other species, the Prairie Rose, the Swamp Rose, the Sweetbriar and many others. All of these species, which we presume have descended from the same ancestors originally, are grouped together as the Rose *genus* (plural, *genera*, Fig. 140), the scientific name for which is *Rosa;* and each of the species also has a scientific name of its own, which for the Dog Rosa is *canina*. From the general structure of their flowers, fruit and other organs, we believe that this Rose genus is closely related to other somewhat similar genera, such as the Cherries (*Prunus*), the Apples (*Malus*), the Hawthorns (*Crataegus*), the Blackberries (*Rubus*), the Strawberries (*Fragaria*), and others; and we therefore group all of these genera together into a still larger unit, the *family*, which in this case is the Rose family or *Rosaceae*. This is a large family, containing about 40 genera and 3,000 species. It is evidently similar in many respects to certain other families, notably the Saxifrage family (Saxifragaceae) and the Legume family (Leguminosae). This group of families, which stand somewhat by themselves and are probably all related to one another by descent, we call an *order*, in this case the *Rosales*.* The Rosales are one of a large number of orders which constitute the great *class* of *Dicotyledoneae* or dicotyledonous plants. This is clearly distinguished from another great class, the *Monocotyledoneae* or monocotyledonous plants; and these two classes comprise the *subdivision* which we call the *Angiospermae* or angiosperms. The angiosperms, together with the more ancient but now much smaller subdivision *Gymnospermae*, or gymnosperms, make up the *division* known as the *Spermatophyta* or seed plants, with which we have already become acquainted as one of the four main groups into which the plant kingdom is divided.

* In general, the scientific name of a family has the ending *-ceae*, that of an order, *-ales*.

These units of classification which we have illustrated include the most important ones, but large groups are often subdivided still further for purposes of convenience, so that we meet with the terms *variety, tribe, section, sub-family* and others, each of which has its assigned place in the system. Every one of the thousands of groups in the plant kingdom has its own peculiar and distinctive characteristics in which it differs from every other group of similar grade, so that a botanist is able to place a newly discovered species in just the particular niche which it should occupy with reference to the plant kingdom as a whole.

Nomenclature.—The technical names for these various groups are derived from the Latin and Greek tongues, and although many plants have "common" names in the language of the country where they grow, the advantages of technical or "scientific" names are so great that they are almost exclusively used by botanists.

In earlier days, before our present system of naming plants had been introduced, the common way in which a botanist referred to a given species was to use a cumbrous descriptive phrase, usually consisting of several Latin nouns and adjectives. As different men often used different words, it frequently became a matter of doubt as to just what plant they were talking about, and much confusion resulted. It remained for the genius of the great Swedish naturalist, Linnaeus, to devise a method which should be simple and uniform. He invented the *Binomial* system of nomenclature, so called because each species is given two names; first, the name of genus of which it is a member, or its *generic* name, and following this a name applied distinctively to the particular species in question, or its *specific* name. The scientific name of the Dog Rose would thus be *Rosa canina.* This system is very much like that used by us in naming individuals, where the "surname" is that of a person's family and the "given name" is distinctively his own. In plants, this order is simply reversed, the surname (generic name) coming first. The binomial system was first used extensively for plants in the "Species Plantarum", a great work published by Linnaeus in 1753, in which he described all plant species then known. This book is the foundation upon which our modern system of plant nomenclature is based.

In order to avoid confusion and to make perfectly clear what plant is meant, there is placed after the plant name the name

(or its abbreviation) of the botanist who first used this name for the species in question. Thus the full name of the Dog Rose is *Rosa canina* L., which means that this particular name was conferred on the plant by Linnaeus. Disputes still arise as to just what certain species should be called, for different botanists have sometimes given different names to the same plant. Such questions must be settled by the adoption of universal rules and practices, and it is to be hoped that through them the nomenclature of plants may in time become perfectly uniform throughout the world.

With this introduction to the history, classification, and nomenclature of plants, we shall proceed in the next four chapters to describe briefly the main features of the four great divisions of the vegetable kingdom.

QUESTIONS FOR THOUGHT AND DISCUSSION

639. Do you think that the first organisms to appear on the earth were more nearly like plants or like animals? Why?

640. It is generally agreed that the earliest plants lived in the water. What evidence can you think of for this?

641. Do you think that the earliest plants were motile or not? Why?

642. What are the advantages and the disadvantages of a many-celled as compared with a single-celled plant?

643. What basis would you use to determine whether a group of cells is a colony or a single plant?

644. In what way is an animal individual a more distinct and definite thing than a plant individual?

645. Why is the increased size of the plant body, beyond a certain point, necessarily followed by the beginning of differentiation?

646. Why were the sexual cells the first ones to become differentiated from the ordinary body cells of the plant?

647. In general, is there a higher degree of differentiation in the body of a water plant or of a land plant? Explain.

648. State all the resemblances you can find between a plant and a civilized nation.

649. What other advantages can you think of, aside from increased vigor, which sexual reproduction might possess over asexual?

650. In sexual reproduction, what is the advantage in having the two types of gametes (male and female) so radically different from one another?

651. Gametes, particularly male gametes, are often motile when all the other cells of the plant are not. How do you think that this has come about?

652. What various advantages and disadvantages can you think of in a life-cycle which shows an alternation of generations?

653. Why do you think it is that the alternation of generations, so well marked in lower plants, has practically disappeared in the highest ones?

654. Do you think that plants or animals were the first organisms to migrate from the sea to the land? Why?

655. When the first plants invaded the dry land, with what kind of soil did they probably find it covered? What important changes did the presence of plant life make in the soil?

656. Give a description of the probable appearance of the land surface before the evolution of the Pteridophytes. What regions on earth today do you think it most closely resembled?

657. What effect did the evolution of the Pteridophytes probably have on the abundance of land animals? Why?

658. Many fungi now live entirely on land. Do you think that they were the first land plants? Explain.

659. What are the advantages of the seed over the spore as an agency for reproduction?

660. Why have seed plants largely superseded pteridophytes?

661. In what way has the evolution of seed plants probably changed the characteristics of plant-eating animals?

662. What is the *practical* use of having a definite system of classifying plants into species, genera, families, and other groups?

663. What organs are chiefly used as a basis for the classification of plants? Why?

664. What is an "artificial" as opposed to a "natural" system of classification?

665. Classify the following objects into a system of "groups within groups," stating briefly the characteristics by which each group may

be distinguished from its coordinate groups, and making in this way what is commonly known as a "key" to these objects: Apple, oak log, pumpkin, maple leaf, cotton fiber, apple blossom, potato, tulip bulb, peanut, turnip, pine cone, peach, spruce shingle, strawberry, automobile tire, squash seed, blade of grass, strip of birch bark.

666. In describing the plant kingdom in the later chapters of this book, much more space, relative to their number of species, has been given many of the lower groups than has been given the angiosperms. Why is this justifiable?

667. State what advantages and disadvantages the scientific name of a plant has as compared with its "common" name.

668. In popular literature we often find that when the scientific name of an animal or plant is mentioned, it has an article in front of it, as, for example, "the *Solanum tuberosum*." Why is this incorrect?

REFERENCE PROBLEMS

108. What is meant by the "life-history" of a plant species?

109. Who was chiefly responsible for the establishment of our modern conception of the Alternation of Generations?

110. In general, how do characters which distinguish the larger groups of plants, such as orders and families, differ from those which distinguish smaller ones, such as genera and species?

111. Why is it that Latin and Greek are the languages from which the scientific names of plants and animals have been chiefly derived?

112. What is the scientific name of the American Elm? of the Paper Birch? of the Apple? of the Cowslip? of the Blue Flag?

113. Find the species, genus, family, order, class, subdivision and division to which each of the following plants belongs, and give the correct scientific name of each: The White Pine; the Red Oak; the Common Field Daisy; the Tiger Lily.

114. If two botanists each give a different name to the same plant species, what is it that determines which name shall be accepted as the correct one?

115. What is meant by the "flora" of a region? by the "moss flora" of a region? by the "forest flora" of a region?

116. Give the derivation of the following terms and explain in what way each is appropriate:

Gamete	Sporophyte	Genus
Zygote	Gametophyte	Species

CHAPTER XIV

THE THALLOPHYTA

The most simple and primitive of the four divisions of the plant kingdom are the *Thallophyta* or thallophytes. This is a huge assemblage of species, about 80,000 in all, which display a wide variety in their structure and life histories. The name "thallus-plants" refers to the character of their vegetative body, which is typically a *thallus*, or mass of tissue with little differentiation into such diverse organs as we find among the higher plants. It is usually rather small, and is often minute. This simplicity of their vegetative structures, together with their generally simple and primitive methods of reproduction, are the chief features which distinguish the thallophytes as a whole.

To construct a truly natural classification for such a heterogeneous group is a very difficult task indeed. The division as a whole is usually separated into two main series: The *Algae*, which possess chlorophyll or a similar substance and may thus live independently, and which include all the seaweeds, together with the pond scums and similar plants of fresh water; and the *Fungi*, which lack chlorophyll and can therefore exist only as saprophytes or parasites, and to which belong the multitude of bacteria, molds, mildews, blights, rusts, toadstools, and mushrooms. The fungi have evidently arisen from several different groups of algae, so that the two series parallel one another somewhat in their various characteristics. It is more convenient to treat each separately however, incidentally pointing out such relationships as seem clear between various groups in the two series.

THE ALGAE

The algae are commonly divided into four classes, the Blue-green Algae, the Green Algae, the Brown Algae, and the Red Algae. The differences in color which have given rise to these names are incidental and are accompanied by more deeply seated distinctions.

Cyanophyceae or Blue-green Algae.—These are the simplest and lowliest of all green plants. The body consists of a single cell, but in most species the cells tend to hold together in colonies. The cell itself is very simple, lacking the nucleus, sap-cavity, and chloroplastids so characteristic of other green plants. Its cytoplasm may be perfectly homogeneous, with the pigment evenly dispersed, or a colored outer zone and a colorless inner one may be roughly distinguishable. The latter perhaps represents a nucleus. The pigment, which seems to be dissolved directly in the cytoplasm and never confined to definite plastids, is usually (though not always) blue-green in color and is probably a combination of chlorophyll with a blue pigment, *phycocyanin*. Both of these may be concerned with photosynthesis but this is as yet uncertain, for our knowledge of the photosynthetic process in the blue-green algae is far less complete than it is for higher plants. The cell-wall is typically thick and mucilaginous, and in many species a group of cells becomes embedded in the gelatinous mass derived from their walls so that a large, jelly-like colony results. On the occurrence of unfavorable conditions for growth, heavy-walled "resting cells" may be produced. Cell division is very simple and shows none of the elaborate phenomena of mitosis, the cell merely becoming constricted by the growth of a new wall until complete separation into two cells takes place. Little differentiation is evident, although peculiar large, dead cells frequently appear in certain species. Reproduction consists merely in cell division or "fission," and no instances of sexuality have ever been observed in the class. In this respect the blue-greens differ from other algae but resemble bacteria, and these two groups have therefore sometimes been placed together as a separate division of the plant kingdom, the *Schizophyta* or Fission Plants, divided into the classes Schizophyceae (Cyanophyceae) and Schizomycetes (Bacteria).

The blue-green algae live in both salt and fresh water and are able to grow at higher temperatures than can any other plants, often thriving in the water of hot springs at temperatures up to 60°C. Most species prefer water which is dirty and full of organic matter, and some may even be found on damp soil, rocks, and other places which are exposed to the air.

One of the simplest examples is *Gloeocapsa* (Fig. 141, B), a minute, single-celled alga with a very gelatinous wall. As an individual divides, the resulting cells of the first generation, and

sometimes those of the third and fourth, are held together, embedded in their swollen cell-walls. In *Nostoc* (Figs. 141, C and D) the individuals are joined loosely into filaments which somewhat resemble strings of beads, and these may also be embedded in a jelly-like substance, the whole colony often reaching a diameter of one centimeter and containing hundreds of filaments.

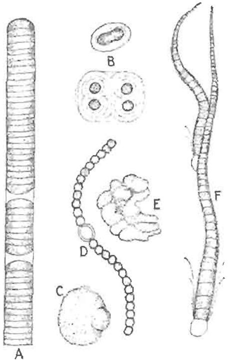


FIG. 141.—Cyanophyceae of various sorts. *A*, *Oscillatoria*, × 340. *B*, *Gloeocapsa*. × 450. *C*, *Nostoc* colony, natural size. *D*, filament of *Nostoc*, with a heterocyst in the middle of it. × 460. *E*, colony of *Rivularia*. × ½. *F*, filament of *Rivularia*, with heterocyst at base. × 225. (*E* and *F after Engler and Prantl*).

Here and there along the filament are frequently found large, empty cells called *heterocysts*. Their function is not definitely known but they may be concerned in breaking up the filament into short segments or *hormogonia*. In *Oscillatoria* (Fig. 141, A) the cells are pressed flatly against one another and the gelatinous wall is so poorly developed that the filaments are free in the water, where they sway or revolve slowly. It is hard to know whether to regard the filament of some of these blue-green algae as a colony of distinct individuals or as a single, many-celled plant.

Chlorophyceae or Green Algae.—This class is by far the largest of the four groups of algae and its members are very diverse. They contain chlorophyll but no other pigment, and the bright

green color which the plant body thus displays has given the class its name. It is well represented in both fresh and salt water and a few species thrive in damp situations on land. The cell is much more highly differentiated here than among the blue-green algae, possessing a nucleus, one or more chloroplasts (often called *chromatophores*) and usually a sap-cavity, thus resembling in its essential details the cells of the higher plants. *Pyrenoids*, or centers of starch formation, are prominent in the chloroplasts. The plant body may consist of a single cell, a filament, or a plate of cells. Most species (though not all) produce *zoöspores*, motile reproductive cells which swim about by the aid of one or more lashes or *cilia* and which grow directly into new plants. These are developed in modified cells or *sporangia*. Various types of sexual reproduction are also found in this class, ranging from instances where the gametes are entirely similar to those where they have become markedly distinguishable as *sperms* and *eggs*. Because of all this structural diversity and of the fact that they are thought to be near the main line of ascent from lower algae to bryophytes, the Chlorophyceae have received intensive study, particularly with regard to the development of the multicellular individual and the evolution of sex.

To classify this great class thoroughly it is necessary to distinguish within it a large number of orders, but for the purposes of our brief survey we can conveniently group these into five: The *Protococcales*, the *Confervales*, the *Conjugales*, the *Siphonales*, and the *Charales*.

1. *Protococcales or One-celled Green Algae.*—These are chiefly microscopic plants. The individuals are single-celled and they may be completely separate or loosely joined into colonies, and are either motile or non-motile.

FIG. 142.—*Pleurococcus*. Single cell and two small groups of cells. × 800.

Pleurococcus (Fig. 142), which forms the green stain found on damp bark, rocks, and similar places, is perhaps the most common type. It consists of a single cell containing one large chloroplastid and reproduces only by cell division. The daughter cells may sometimes cohere for a time in small groups. This is one of the algae which is commonly associated with various fungi to form the peculiar group of *lichens*.

Chlamydomonas (Fig. 143) is a motile type, its cells containing a single chloroplastid, a red pigment spot, some contractile vacuoles, and two cilia.* The cell may lose its cilia and divide into several zoöspores, each of which is capable of producing a new plant. Toward the end of the growing season, however, smaller motile

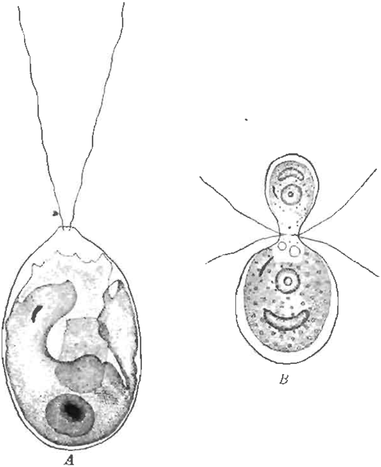


FIG. 143.—*Chlamydomonas*. *A*, individual plant, showing the large chloroplast, the pyrenoid, the nucleus and the two cilia. *B*, union of two gametes. In most instances these gametes are equal in size, but in the case figured they are distinctly different. (*A after G. S. Torrey. B after Goroschankin*).

cells are formed which swim about and unite in pairs. These are the *gametes*, and in this case their evolution from ordinary zoöspores seems to be very clear. The cell formed by their union is known as a *zygospore*, a term applied to all cells produced by the fusion of similar gametes. Such a form of sexual reproduction is known as *isogamy*.

* This plant is very similar to members of the interesting group of Flagellates, sometimes classed with animals and sometimes with plants, and which are evidently intermediate between the two.

There are a number of other algae similar to *Chlamydomonas* except that they are united into loose colonies of ciliated individuals, and the group culminates in the large, hollow, spherical colonies of *Volvox* (Fig. 144) which often consist of thousands

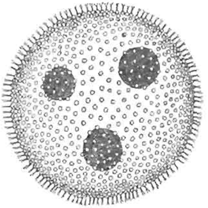


FIG. 144.—*Volvox*. Globular colony of biciliate individuals, with three daughter-colonies developing in its interior.

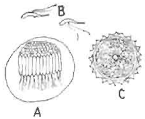


FIG. 145.—*Volvox*. *A*, group of sperms developed within a single cell. *B*, sperms. *C*, fertilized egg or oöspore. (*After Cohn*).

of cells. In these higher forms the sperms are markedly different from the eggs, and the cell formed by their union is termed (as in all such cases) a *fertilized egg* or *oöspore* (Fig. 145). Sexual

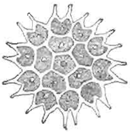


FIG. 146.—*Pediastrum*. A group of sixteen cells united into a plate-like colony. × 260.

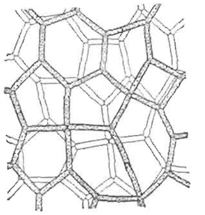


FIG. 147.—*Hydrodictyon*. Portion of a net-like colony, individual cells forming the meshes of the net. × 310.

reproduction of this type is known as *heterogamy*. It should be noted that both zygospores and oöspores are typically thick-walled cells which are capable of resisting such unfavorable conditions as drought and low temperature, and of germinating to

produce new plants whenever a suitable environment again appears.

In another group of Protococcales the body cells are non-motile, independent movement being limited here to the zoöspores and the gametes. The individuals are grouped in colonies which are simple, few-celled plates in *Pediastrum* (Fig. 146) but form a complex network in the water-net, *Hydrodictyon* (Fig. 147). The zoöspores do not escape from the mother plant and swim about, as is usually the case, but the group of zoöspores formed within a single mother-cell displays the remarkable habit of uniting, while still within this cell, to form a minute colony of non-motile cells which is finally liberated and grows into a mature colony.

The Protococcales are of especial interest because of the light which they throw upon the development of the multicellular individual and the differentiation of the sexes.

2. *Confervales or Conferva-like Algae.*—These include most of the common thread-like and membranous green algae of salt and fresh water. They all reproduce asexually by zoöspores and also exhibit various types of sexual reproduction, simple in the lower forms but relatively complex in the higher ones. The order is large and varied and contains many species which are but distantly related to one another. Three typical genera will give us an idea of the group.

Ulothrix (Fig. 148) is a common thread-like or *filamentous* alga, its short cells each containing a single nucleus and one large chloroplast. The contents of any cell may become divided into a group of zoöspores which escape and may each form a new plant; and smaller binucleate motile cells, produced in the same manner as the zoöspores and often indistinguishable from them, act as gametes and conjugate in pairs to produce zygospores. *Ulothrix* is often cited as another good example of the origin of sexual reproduction.

Oedogonium (Fig. 149) is also a common genus and its filament is anchored by a modified basal cell, the *holdfast*. In certain cells the contents may round up and produce a single large zoöspore with a circle of cilia near one end, and this soon settles down, develops a holdfast, and grows into a new filament. Other cells also become much enlarged, each producing a single rounded, non-ciliated cell, well supplied with chloroplastids and food material. This is the female gamete or egg, and the cell which

produces it (like all egg-producing structures in these lower plants) is termed an *oögonium*. In other cells the contents divide into two small, motile male gametes or sperms, and each of these mother-cells (like all structures which produce male gametes) is known as an *antheridium*. One of the sperms enters an egg

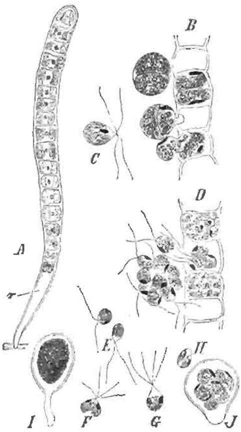


FIG. 148.

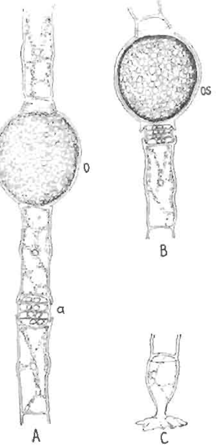


FIG. 149.

FIG. 148.—*Ulothrix*. *A*, young filament with rhizoid cell (*r*) by which it is attached. *B*, portion of filament with escaping zoöspores. *C*, single zoöspore. *D*, formation and escape of gametes. *E*, gametes. *F* and *G*, stage in the conjugation of two gametes. *H*, zygote or zygospore. *I*, zygote beginning to germinate. *J*, group of zoöspores produced by a zygote. (*From Strasburger, after Dodel-Port*).

FIG. 149.—*Oedogonium nodulosum*. *A*, filament with antheridium (*a*), each cell of which produces two sperms: and oögonium (*o*), containing one large egg. *B*, filament with a thick-walledo öspore (*os*) which has developed from a fertilized egg. *C*, basal cell of a filament, showing *holdfast*. All × 300.

and fertilizes it, and the oöspore thus formed germinates into a group of zoöspores.

Coleochaete (Fig. 150) is a fresh-water alga the vegetative body of which consists of a flat plate or cushion of radiating filaments. Its cells may produce single, large, biciliate zoöspores. Antheri-

dia and oögonia are formed much as in *Oedogonium*, and a thick-walled oöspore is produced. Following this, however, the adjacent cells give rise to branches which grow up and surround the oöspore, *forming a distinct spore case or fruiting body*. The oöspore germinates into a group of cells each of which ultimately forms a zoöspore. This reproductive cycle foreshadows the "alternation of generations" of the higher plants. In its struc-

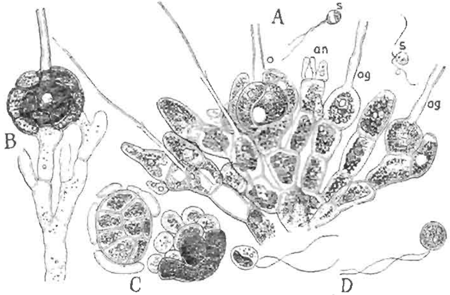


FIG. 150.—*Coleochaete*. *A*, portion of fertile thallus. *og*, oögonium, containing a single large egg. *an*, antheridium. *s*, sperm. *o*, oöspore or fertilized egg, which is beginning to be surrounded by filaments growing up from below. *B*, mature fructification, the oöspore surrounded by an envelope of cells. *C*, the contents of the fructification dividing up into zoöspores. *D*, zoöspores. (*From Goebel, after Pringsheim*).

ture and life history, *Coleochaete* is the most specialized of the green algae and is believed by many botanists to approach the lowest bryophytes.

3. *Siphonales or Tubular Algae.*—These are distinguished from all other algae by the fact that the whole plant body, whether it be a simple filament or a well-differentiated thallus, is essentially a *single cell*. The cross walls which divide other algae and all ordinary plants into small cells are absent, and the mass of cytoplasm with its thousands of nuclei is therefore able to circulate freely throughout the whole plant. Such a multinucleate cell, of which these plants are extreme examples, is known as a *coenocyte*.

The Siphonales are chiefly marine forms, especially abundant in the warmer seas. They usually produce zoöspores and in

cases where sexuality has been proven are always isogamous except in the genus *Vaucheria*, which is such a familiar and distinctive type that we shall describe it more fully. This alga forms the common "green felt" so often found on damp soil or in muddy pools, and consists of a tangled mass of coarse, branch-

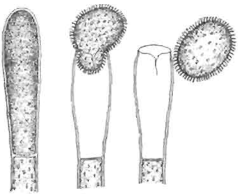


FIG. 151.—*Vaucheria*. Asexual reproduction. The tip of a filament is cut off by a wall and its contents becomes a large zoöspore, with many nuclei and many groups of paired cilia. The zoöspore breaks through the wall and escapes. (*After Gotz.*)

ing, tubular filaments. Large zoöspores are produced, each of which is merely the contents of the tip of a filament which has been cut off by a wall and has escaped (Fig. 151). The sexual organs are not simply modified vegetative cells, as in the plants

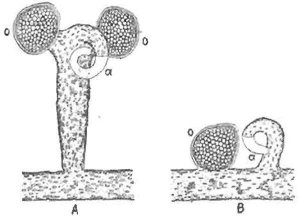


FIG. 152.—*Vaucheria*. Sexual reproduction. Oögonia, *o*, each contain a single egg. Antheridia, *a*, have discharged all their sperms and are empty. *A*, *V. terrestris*. *B*, *V. sessilis* × 130.

previously studied, but are specialized for gamete production (Fig. 152). A cell partitioned off by a wall from the main filament or from a small lateral branch becomes the oögonium, within which a single, large egg is formed. From the tip of another

small branch near by is cut off a cell which develops into an antheridium. One of the sperms here developed enters the oögonium and fertilizes the egg, producing a heavy-walled oöspore.

4. *Conjugales, the Pond Scums, Desmids, and Diatoms.*—The plant body of these algae is a single cell or an unbranched filament. The species are all confined to fresh water and are dis-

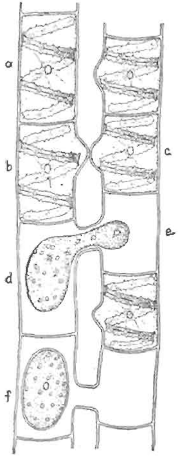


FIG. 153.—*Spirogyra.* Two adjacent filaments, showing stages in sexual reproduction. Cell *a* shows the normal, resting condition, with the spirally placed, band-like chromatophore, in which numerous circular pyrenoids can be seen. Cells *b* and *c* are sending out conjugating tubes to each other. The contents of cells *d* and *e* have contracted somewhat and the contents of *e* is passing over through the conjugating tube and uniting with *d*. At *f* is shown the mature zygospore which has arisen from the union of two cells. × 150.

tinguished from other Chlorophyceae by the absence of zoöspores or other means of asexual reproduction, the absence of motile cells of any sort, the occurrence of large and conspicuous chloroplastids, and the characteristic manner in which sexual reproduction is brought about.

The Pond Scums, of which *Spirogyra* (Fig. 153) is the common example, are all filamentous algae. In this genus the chloroplast is a broad, strap-shaped structure running spirally around the cell and on it appear a series of small, rounded areas, the pyrenoids. The nucleus is suspended in the middle of the sap cavity by threads of cytoplasm extending to the walls. In sexual reproduction, adjacent cells of two filaments which are lying side by side

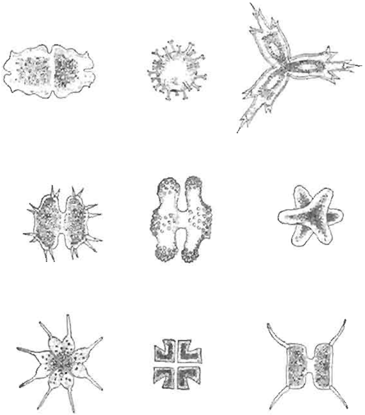


FIG. 154.—Desmids of various types.

send out projections or "conjugating tubes" toward one another. The tips of these touch, the wall between them breaks down, and through the channel thus formed the whole protoplasmic contents of one cell enters the other and the living portions of the two cells fuse into a thick-walled zygospore. Occasionally the two cells conjugate in the tube itself, and sometimes two adjacent cells of the same filament may unite.

The Desmids (Fig. 154) are unicellular plants of the utmost variety and beauty of form. The cell is composed of two perfectly symmetrical halves separated by a zone, the *isthmus* which is often constricted and under which lies the nucleus. Aside

from ordinary cell division, reproduction is effected by conjugation between two protoplasts, each of which has escaped from its wall.

The Diatoms (Fig. 155), a large group of unicellular plants of somewhat uncertain relationship, can perhaps best be considered here. They are represented by thousands of species in salt and fresh water and are the most abundant of the minute plants which make up that multitude of freely swimming or float-

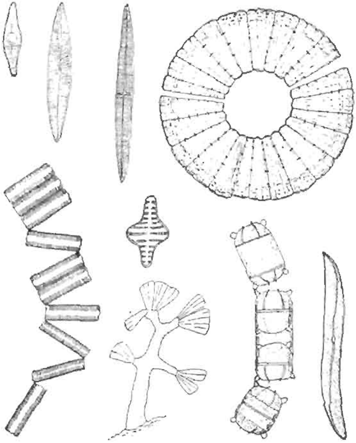


FIG. 155.—Diatoms of various types.

ing algae in the open sea and in fresh water which we know as the *plankton*. Many species are also sessile and may be united into filaments or other colonies. The wall is hard and flinty, being heavily filled with silica, and consists of two halves or *valves* one of which fits over the other like a box cover. These are highly diversified in shape and are frequently ornamented with minute and intricate markings which have long been the delight of microscopists. The color of most diatoms is brown owing to the presence of a pigment, *diatomin*, in addition to chlorophyll.

5. *Charales or Stoneworts* (Fig. 156).—This remarkable group of plants stands apart from all others and we have no certain knowledge as to its relationships. The vegetative body consists of long, jointed stems, and at the joints, or nodes, arise whorls of

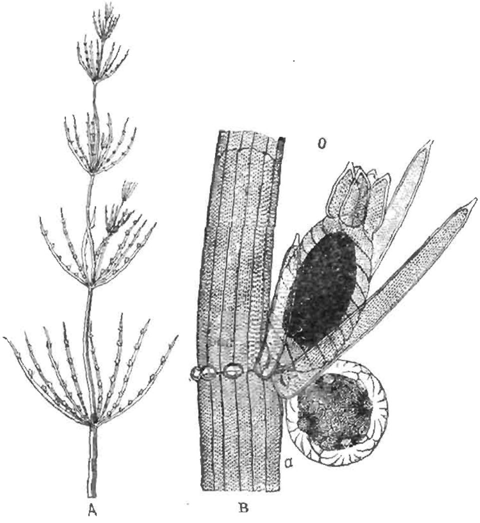


FIG. 156.—*Chara*. *A*, a main branch, showing the circles of small, lateral branches, bearing the sexual organs, arising at the joints of the main branch. *B*, a portion of a branch, showing the main axis and the short side branches, near the union of which are attached an antheridium (*a*) and an oögonium (*o*). (*B* after Sachs).

short branches. No asexual spores are produced, but along the branches are borne antheridia and oögonia, far more complicated than among any other thallophytes. The antheridium is spherical and its wall is composed of eight somewhat triangular cells from the inner surface of which arise a large number of many-

celled, sperm-producing filaments. The oögonium is covered with a wall or envelope of spirally wound cells growing up from the tissue below it, and produces a single large egg. After fertilization the envelope hardens, forming a nut-like spore case around the oöspore. The absence of anything suggesting an alternation of generations indicates that these plants should be placed among the thallophytes, but they are clearly distinct from any other members of the division.

Phaeophyceae or Brown Algae.—These plants may be distinguished from other algae by their characteristic brown color, due to one or more brown pigments associated with chlorophyll, and by certain structural characters. The Phaeophyceae are the largest and rankest of all algae and display the highest degree of bodily differentiation. They are found almost exclusively in salt water and are best developed in the cooler seas. Thriving most commonly in shallow water and the zone between tide marks, they are subjected to the buffeting of the waves and may be exposed to the air for several hours a day. These plants probably represent an entirely independent line of evolution from the green algae and seem to have led to no higher types. Two orders are recognized among them, the *Phaeosporales* and the *Fucales*.

1. *Phaeosporales or Kelps and Their Allies.*—In this order occur the kelps (*Laminaria*) common in the north Atlantic and elsewhere, together with many other large algae such as the giant kelp (*Macrocystis*), the sea otter's cabbage (*Nereocystis*), the sea palm (*Postelsia*), and others smaller in size. They are all isogamous and in most cases produce zoöspores.

Ectocarpus (Fig. 157), one of the best known genera, is a rather small, filamentous plant. As in the algae previously studied, the zoöspores are here produced in sporangia which are modified single cells. The gametes, however, are developed in large *multicellular* structures (*plurilocular* sporangia) which begin to show a resemblance to the highly developed sexual organs characteristic of the bryophytes. Each of the many small cells into which the contents of this structure is divided forms one or two gametes which fuse in pairs to produce zygospores. Instances have been observed in which these gametes germinate directly into a new plant, and thus function essentially like zoöspores, which they also resemble structurally. Gametes of different size sometimes unite, thus indicating the beginning of

a heterogamous condition. In genera like *Ectocarpus* we are evidently near the beginning of sexuality in the brown algae.

The larger forms or kelps may become huge plants, the giant kelp sometimes attaining a length of from two hundred to three hundred meters. They are attached to the rocks by massive holdfasts. The stout "stems" or *stipes* support broad and

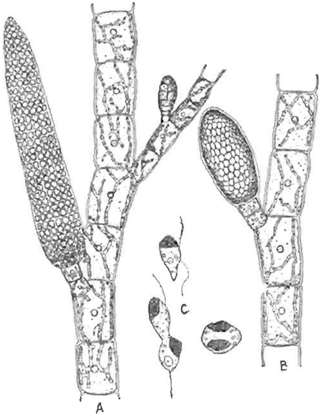


FIG. 157.—*Ectocarpus*. *A*, filament with multicellular or *plurilocular* sporangia, in which gametes are produced. A young and growing sporangium is shown above. *B*, filament with a single-celled sporangium, in which zoöspores are produced. *C*, various stages in the union of two gametes. Above, a single gamete; at left, the beginning of union; at right, the resulting zygospore. × 375. (*C after Oltmanns*).

frequently much-divided blades and often display a certain degree of structural differentiation. The abundant gametes were long thought to be zoöspores, but their true nature as sexual cells is now known and it may be that zoöspores are rather rare in this group.

2. *Fucales or Rockweeds*.—These plants differ from the kelps in producing no zoöspores and in displaying a heterogamous type of sexual reproduction.

Fucus, the best known genus, is exceedingly abundant on rocks between tide marks in the temperate regions. The vegetative body of this alga is a flat, repeatedly forking thallus well provided with air bladders (Fig. 158). The swollen tips of certain

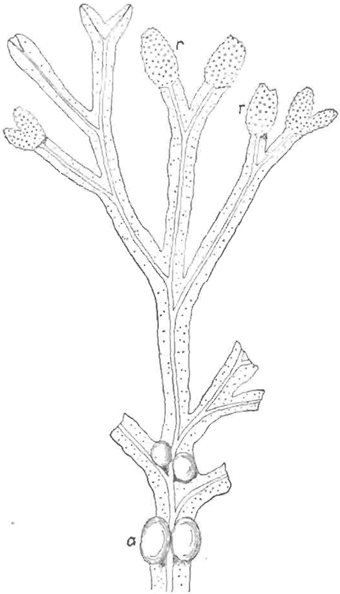


FIG. 158.—*Fucus vesiculosus*. Portion of thallus showing air-bladders (*a*) and receptacles (*r*). On the surface of the latter are the many small openings of the conceptacles.

branches are known as *receptacles* and bear the sexual organs. Scattered over these tips and just below the surface are many small chambers or *conceptacles* each opening to the outside by a pore. Lining the wall of these chambers are masses of branch-

ing filaments among which are placed the antheridia and oögonia (Fig. 159). The antheridia are small cells arising on branches of the filaments and producing swarms of biciliate sperms. The oögonia are larger cells, the contents of each dividing into eight

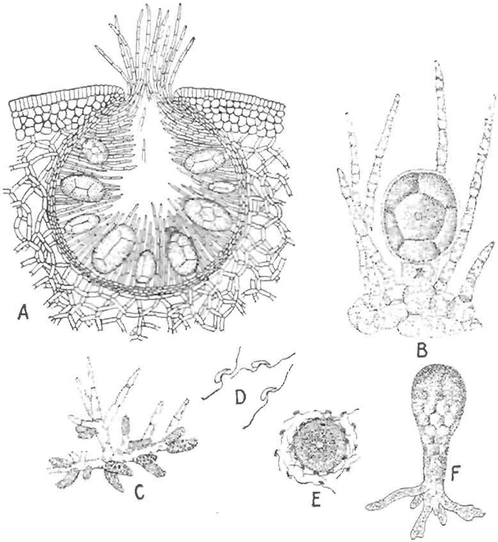


FIG. 159.—*Fucus*. *A*, female conceptacle, with oögonia and sterile filaments. *B*, single oögonium at maturity, containing eight eggs. *C*, group of antheridia from a male conceptacle. *D*, sperms. *E*, egg after discharge into the water, surrounded by sperms. *F*, young plant arising from an oöspore. (*B, C, D, E and F after Thuret*).

eggs. In some species both sex organs are produced in the same conceptacle, in others they occur in different conceptacles on the same plant, and in still others the whole plant is entirely male or entirely female. Both eggs and sperms are discharged from the mouth of the conceptacle and fertilization takes place in the open

water outside. The oöspore settles to the bottc itself, and develops directly into a new plant.

Rhodophyceae or Red Algae.—These are a group, rich in species, almost exclusively marine, : their best development in the warmer seas. Most c entirely submersed, below tide marks, and are t

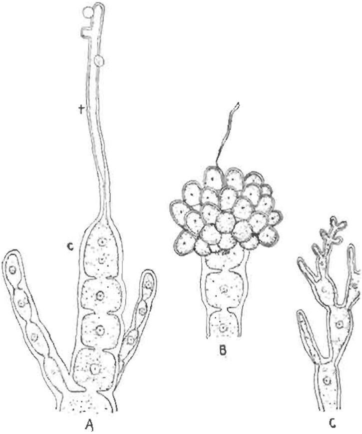


Fig. 160.—*Nemalion.* *A*, procarp at end of a filament. *c*, ca *t*, trichogyne, to which several sperms are attached. A male nucl the carpogonium. *B*, cystocarp, which has arisen from the ferti *ium. Carpospores are developing at the ends of short filaments.* groups of small cells each of which produces a sperm. × 60.

particularly conspicuous or familiar. The vegetativ to be delicate, filamentous, and much-branched, in the bulky thallus of the brown algae. The Rhodo distinguished from all other algae by their character color (due to the pigment *phycoerythrin* which is p chlorophyll); by the complete absence of motile cells and by a highly specialized type of sexual reproduc do not include primitive types but seem to have ai

point already well up in the scale of algal evolution. The higher members of the class display an unquestionable alternation of generations. Two typical genera will illustrate the complexities of reproduction in this group.

Nemalion (Fig. 160) is a common form with a branching, filamentous habit and represents the simplest of the red algae. The numerous small antheridia produce non-motile,

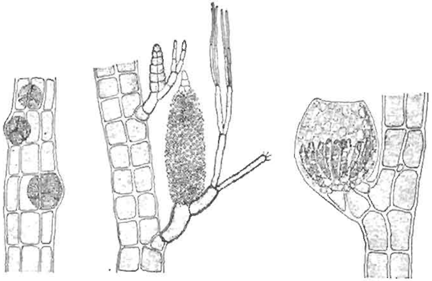


FIG. 161.—*Polysiphonia fibrillosa.* *A*, Portion of a tetrasporic plant showing three groups of tetraspores. These spores occur in *tetrads* or groups of four. × 90. *B*, portion of a male plant. Above, an immature antheridium; below, a mature one, producing large numbers of sperms on its surface. × 215. *C*, portion of a female plant showing a ripe cystocarp, its wall enclosing a group of carpospores. × 45.

binucleate sperms. The female sexual organ, which is here called the *procarp*, consists of two cells—a basal *carpogonium*, containing the single female cell and homologous with the oögonium of other algae; and a terminal cell, the *trichogyne*, which is drawn out into a hairlike tip. The sperm is carried by water currents to the trichogyne, down which its contents passes into the carpogonium. The fertilized carpogonium does not develop a new plant directly, but produces a group of short filaments on the end of each of which is borne a non-motile *carpospore*. This whole structure of spores, filaments, and carpogonium is known as the *cystocarp*. A carpospore germinates directly into a new plant.

Polysiphonia (Fig. 161), another common member of the class, displays a much more complex sexual history and is typical of

the majority of the red algae. Three types of plants, similar in vegetative structure but differing in their reproductive organs, may be distinguished: Male plants, producing antheridia only; female plants, producing procarps only; and sexless *tetrasporic* plants, producing sporangia in each of which are four asexual *tetraspores.* The procarp is somewhat more complex than in *Nemalion* since it contains a group of *auxiliary cells.* Fertilization, however, occurs in much the same way, a sperm coming in contact with the trichogyne, entering the carpogonium, and fusing with the female nucleus. Some rather complicated fusions now take place between the fertilized carpogonium and the auxiliary cells, as a result of which sixty or more carpospores are produced. An envelope of sterile cells grows up from the base and encloses this spore mass, forming the cystocarp.

Experiment has established the fact that these carpospores produce only tetrasporic plants, and that the tetraspores in turn produce only male or female plants. Thus a regular alternation of sexual and non-sexual individuals is set up. Cytological examination has further proven that the tetrasporic plants have twice the number of chromosomes possessed by the sexual plants, and there seems no reason to doubt that we are dealing here with a true alternation of generations, the tetrasporic plant (plus the cystocarp) being a sporophyte, and the sexual plants, gametophytes. This is the more remarkable since all the plants are perfectly similar in their vegetative structures.

The red algae are very evidently a specialized class and although they have reached a marked degree of complexity, they apparently have not been the ancestors of anything higher up in the evolutionary series.

THE FUNGI

The other great group of the thallophytes are the fungi, which are distinguished from algae by the absence of chlorophyll. Their consequent inability to manufacture food therefore compels fungi to live either as *saprophytes* or as *parasites.* Like the algae, this is a heterogeneous group and many of its members seem more closely related to certain groups of algae than to other fungi, but as a matter of convenience and custom, and in the absence of any widely accepted "natural" classification of the thallophytes, they will all be considered together. This immense array of lowly plants is much more numerous in species than the algae and

contains hundreds of types which are of the utmost importance to man and which form the subject matter of various special sciences, notably bacteriology and plant pathology.

In the general morphology of both their vegetative and their reproductive structures the fungi rather clearly parallel the algae, ranging from strictly unicellular types in the bacteria, through filamentous forms, to those which have a large and rather complex plant body; and displaying various types of

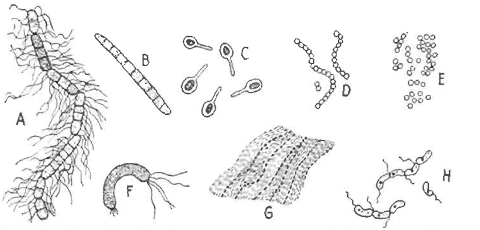


FIG. 162.—Bacteria of various types. *A*, motile individuals of *Bacillus subtilis*. *B*, non-motile individuals of *Bacillus subtilis*. *C*, tetanus cocci. *D*, erysipelas cocci. *E*, pus cocci. *F*, *Spirillum undula*. *G*, gelatinous or *zoöglaea* condition of a mass of bacteria. *H*, cholera vibrios.

sexual reproduction, both isogamous and heterogamous. In all fungi above the bacteria, the plant body is composed of one or more filaments, each of which is known as a *hypha* (plural *hyphae*). The whole mass of hyphae, which are often tangled or matted together, is called the *mycelium*. Special absorbing organs or *haustoria* (singular *haustorium*) are usually developed, through which the plant draws its food from the material or *substratum* on which it grows.

The series may best be divided into four classes: The Bacteria, the Alga-like Fungi, the Sac Fungi and the Basidia Fungi.

Bacteria.—These plants differ from other fungi in being strictly unicellular, although they may sometimes form loose colonies. The cells are usually very small, ranging from about 0.025 mm. to as low as 0.0005 mm. in length, so that bacteria are the smallest of living things. Internally, these cells seem to be almost structureless. There is some evidence, however, that nuclear material and perhaps a vague nuclear body may be present, but the very minute

size of bacteria makes a cytological study of them exceedingly difficult. The cell wall rarely contains cellulose. One or more cilia are found in many species, which thus have the power of active motility. Various structural types are recognized by bacteriologists, of which the commonest are the *coccus* form, which is spherical; the *bacterium* or *bacillus*, which is rod-shaped, and the *spirillum*, which is curved (Fig. 162). The only type of reproduction known is simple cell-division, or fission, which is unaccompanied by any of the complex phenomena found in the higher plants, but which in the presence of an abundant food supply may take place so frequently that a single cell will give rise to millions of individuals in a day's time. At the onset of unfavorable conditions the protoplasm of the cell draws itself together and produces a thick-walled spore which will germinate whenever a favorable environment again ensues. Actively growing bacteria will ordinarily withstand relatively high temperatures but their resting spores are still more resistant and will often be found alive and able to germinate after hours of subjection to boiling water. They can also survive extreme cold and dryness. In their various characteristics, therefore, the bacteria (as we have before noted) show much resemblance to the blue-green algae.

Although bacteria occur in countless myriads of individuals and although their diverse activities make them almost omnipresent in air, water, and soil, they are so small as to be quite invisible and from a practical point of view would be entirely negligible were it not for the profound effects which they produce. Their importance in agriculture, particularly through their activity in the soil and in dairy products; their role as the chief agents of fermentation and decay, and particularly their tremendous direct interest to man as the cause of some of the worst and most prevalent of those diseases which afflict him and his domestic animals and plants, have caused them to be studied with especial thoroughness and have established bacteriology as one of the most active of the sciences.

Our knowledge of bacteria dates only from the latter half of the nineteenth century. Their existence was proven by that great Frenchman, Louis Pasteur (Fig. 163), who labored for years, meeting with the ridicule and antagonism which often greets a new discovery, before he could convince his fellow scientists that such minute objects were actually alive and were

responsible for so many of the happenings of daily life. Since Pasteur's day, as the result of our knowledge of bacteria, the practice of medicine (and to a considerable extent that of certain branches of agriculture and industry) has been radically changed; and the astonishing advances in modern surgery, made possible by Pasteur's discoveries and inaugurated by the great surgeon Lister, have converted this branch of medicine from a dreaded

FIG. 163.—Louis Pasteur, 1822–1895.

last resort to a common and safe means of relief. The bacteriologist of today has developed a complicated and elaborate technique whereby he can isolate individual bacteria, cultivate them artificially on especially prepared and sterilized foods or *media* of various kinds, and study the characteristic appearance of individuals and masses, together with the physiological behaviour peculiar to each. Both as the enemies and as the allies of the human race, these lowly plants with which the bacteriologist works are among the most important members of the vegetable kingdom.

Saprophytic Types.—The saprophytic bacteria live on dead plant or animal material. They are responsible for much of the fermentation which carbohydrate substances often undergo when exposed to the air and which, as a form of incomplete respiration,

we have discussed in our study of metabolism. *Decay*, essentially the same type of process as fermentation except that it takes place in all sorts of organic substances and is carried through to a complete break-down of these substances into carbon dioxide, water, nitrogen, and mineral salts, is brought about almost entirely through the activity of the many types of putrefactive and decay-producing bacteria. All successful methods of preserving food depend on eliminating these bacteria or preventing their activity.

Pathogenic Types.—Those members of the class which are parasitic on other organisms are known as *pathogenic* bacteria. A particular species is the cause of each of the various bacterial diseases, such as diphtheria, tuberculosis, typhoid fever, pneumonia, cholera, and many others among animals and man, as well as pear blight, cucumber wilt, black rot of cabbage, and others among plants. These diseases are often communicated from one individual to another, since the pathogenic bacteria responsible for them may be easily transmitted through air, water, food, or contact. Bacteria which are very minute or otherwise difficult to recognize are also probably responsible for many diseases the cause of which is at present unknown.

The harmful effect of pathogenic bacteria on animals is often not due to the direct attack of the parasite but to the poisonous by-products, or *toxins*, which they secrete and which enter the blood. The afflicted individual will often produce *antitoxins* capable of counteracting the poisonous effect of the toxins and of rendering the individual *immune* for a time to the attacks of this particular parasite. The practice of *vaccination* consists in inoculating an individual with the parasitic bacteria and thus subjecting him to a mild attack of the disease in order to stimulate the production of sufficient antitoxin in his system to confer immunity upon him for a long time. Vaccination is particularly effective against small pox and typhoid fever. The attacks of certain other disease-producing organisms may also be prevented or rendered less virulent by injecting into the circulation a little blood serum from an individual (usually a cow or horse) which has had the disease and whose blood is therefore rich in antitoxin. This *serum* or *antitoxin* treatment has been especially successful with diphtheria, tetanus, and hog cholera.

In our study of the soil we mentioned two other groups of bacteria which are of especial importance to the higher plants

because of their relation to nitrogen (Fig. 18). These are the *nitrogen-fixing* bacteria, which are found in tubercles on the roots of plants belonging to the Legume family and which are able to take nitrogen directly from the air and to incorporate it into their bodies; and the *nitrifying* bacteria which convert ammonia, the end product of protein decay, into nitrite salts and these, in turn, into nitrate salts, the only form in which nitrogen can generally be utilized by green plants.

Phycomycetes or Alga-like Fungi.—These fungi, as their name implies, resemble rather closely certain of the algae, particularly

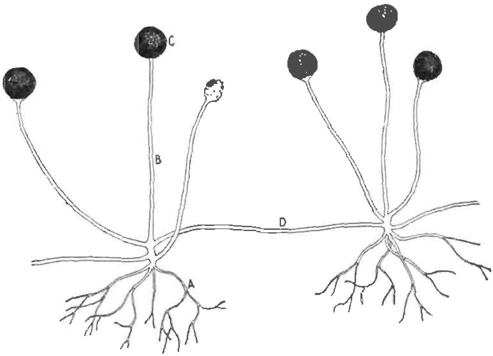


FIG. 164.—The bread-mold (*Rhizopus*). General habit of the plant. The mycelium (*A*) of much-branched hyphae penetrates the substratum and sends up into the air stouter hyphae, the sporangiophores (*B*), on which are borne the spherical sporangia (*C*). One sporangium has burst, shedding its spores, a few of which still adhere to the central axis or *columella* of the sporangium. The two groups of sporangiophores are connected by a *stolon* (*D*).

in their methods of reproduction. They seem especially near the Siphonales because of the fact that their filaments (hyphae) are coenocytic, and it is probably from that general region of the algal series that they originated.

The Phycomycetes include a great many of the forms which we know as *molds* and *blights*. Three orders are particularly notable and we shall describe them briefly. These are the *Mucorales*, the *Saprolegniales*, and the *Peronosporales*.

1. *Mucorales, the True Molds or Black Molds* (Fig. 164).—These fungi are very common on moist, decaying organic material such as manure, rotting fruit, and the like. Their white, cobwebby mycelium, composed of much-branched hyphae, freely penetrates the substratum in all directions. From the surface, stout hyphae arise into the air and bear at their tips globular

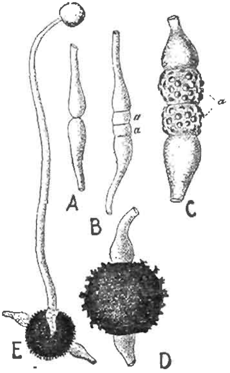


Fig. 165.—*Mucor.* Formation and germination of the zygospore. *A*, two conjugating hyphae in contact. *B*, a gamete, *a*, has been cut off from the end of each hypha. *C*, the enlarged gametes. *D*, thick-walled zygospore which has arisen from a union of the two gametes. *E*, zygospore germinating to form a sporangium. (*From Strasburger, after Brefeld*).

sporangia which burst and liberate masses of dark-colored spores, each of which may germinate directly into a new plant. Sexual reproduction is isogamous or essentially so (Fig. 165). Two short branches or *suspensors*, arising from adjacent hyphae, approach one another and come into contact end-to-end. From the tip of each is cut off a single multinucleate cell which is the gamete, and these two adjacent gametes fuse to produce a thick-walled zygospore. It has been found that two distinct sexual strains often exist, entirely similar outwardly but functioning quite differently in reproduction. These have been called the *plus* and the *minus* strains and correspond to the two sexes, for

zygospores are usually produced only when a *plus* plant and a *minus* plant come into contact. These fungi furnish an interesting example of a physiological differentiation of sex which is not accompanied by morphological differences.

2. *Saprolegniales or Water Molds* (Fig. 166).—In contrast to the Mucorales, this group is entirely aquatic. Its members live on the bodies of dead insects and other animals, and a few are parasitic, attacking fish and amphibians. A cell cut off from

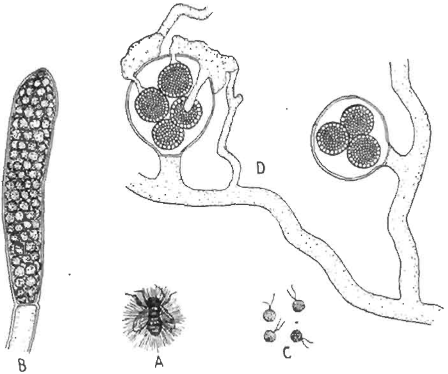


FIG. 166.—*Saprolegnia*, one of the Saprolegniales. *A*, mycelium on an insect in water. *B*, terminal sporangium producing zoöspores. *C*, zoöspores. *D*, sexual organs; the two oögonia each containing several eggs. The one at the left penetrated by antheridial filaments.

the tip of a hypha develops into a sporangium and liberates a large number of motile zoöspores. Sexual reproduction is heterogamous. A single-celled spherical oögonium is developed and produces several eggs which are fertilized by the contents of an *antheridial filament*, a slender branch which grows out from the main hypha near the oögonium and fuses with it. In many cases the eggs develop into mature spores without having been fertilized at all.

Peronosporales or Blights and Downy Mildews (Fig. 167).—The species composing this group are all parasites on the higher

plants. Their spores germinate on the surface of the leaf or stem and, entering the tissues, branch through them in all directions, absorbing food and often causing the death of the host plant. Definite fruiting bodies are produced at the surface of various organs of the host, where specialized hyphae become constricted to form spores, which separate and are carried away

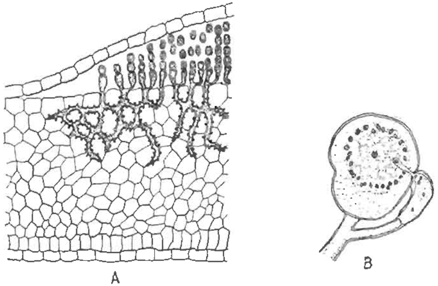


FIG. 167.—*Albugo*, one of the Peronosporales. *A*, section through a leaf-blade showing portion of a "blister" produced by the fungus. The hyphae penetrate between the cells of the leaf, sending into them small, sucker-like structures. Under the epidermis are produced rows of conidia. *B*, sexual organs, the antheridial filament (at right) discharging a male nucleus into the oögonium, at left.

by the wind. Non-sexual, aerial spores produced in this manner are called *conidia*, and are of frequent occurrence among fungi. Sexual organs appear in the deeper tissues. The egg nucleus in the oögonium is fertilized by a male nucleus from an adjacent antheridial filament, and a thick-walled oöspore is formed. Such destructive plant parasites as the potato blight and the grapevine mildew belong to this order.

Ascomycetes or Sac Fungi.—This enormous group of plants includes over 20,000 species. They show but little resemblance to the algae, and although all must have come originally from some chlorophyll-bearing forms, their exact ancestry is not clear. These fungi are typically land-inhabiting plants and include both saprophytic and parasitic species. Both groups differ from the Phycomycetes in the fact that their hyphae are divided into cells by cross-walls, and that sexual processes are much reduced or altogether lacking. The plant body commonly consists

of a much-branched mycelium extending throughout the substratum, and a definite *fruiting body* which is developed at the surface. Each group displays a rather specialized method of spore formation.

The Ascomycetes are distinguished by their production of spore sacs or *asci* (singular, *ascus*) in each of which are borne eight spores, the *ascospores* (Fig. 168). A group of asci are

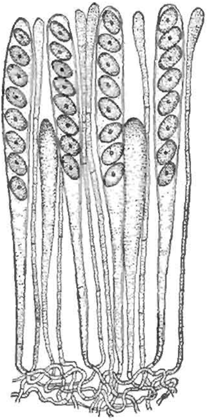


FIG. 168.—Spore production in an ascomycete. Portion of the hymenium, or fruiting surface, of *Peziza*, showing the asci, each with eight ascospores. Among the asci are slender, sterile hairs, or paraphyses, and two young asci.

generally embedded in a mass of sterile hyphae and partially or completely surrounded by a protective envelope of compact mycelium. Such a fruiting body is known as an *ascocarp*. In many cases, this ascocarp has been found to originate as the result of a sexual union deep in the mycelium, the whole process bearing a considerable resemblance to that found among the red algae. The ascomycetes include an immense variety of types, only a few of which can be mentioned here.

1. *Pezizales or Cup Fungi* (Fig. 169).—Throughout this order the ascocarp is a broad disc, cup, or funnel, and the name Dis-

comycetes or disc fungi is therefore often applied to the group. The inner surface of the cup consists of a layer of asci and sterile hyphae. Such a layer is known as the *hymenium*. These plants are almost all saprophytes and their brightly colored fruiting

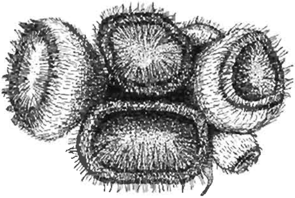


FIG. 169.—*Peziza ciliata*. The cup-like ascocarps, on the inner surface of which the asci are borne.

bodies are conspicuous on rotting logs, damp earth, and similar situations.

Related to the cup fungi are the Morels (*Helvellales*), which develop large, fleshy, and edible fructifications, the fruiting surface of which is broken up into irregular pockets; and the Truffles (*Tuberales*), which produce subterranean, tuber-like ascocarps, usually associated with the roots of oak trees, and much prized as delicacies.

FIG. 170.—*Plowrightia morbosa*, the "black knot" of plums and cherries. Hard, black fruiting mass of the fungus on a twig which it has attacked. The small dots are openings to the perithecia.

2. *Pyrenomycetes or Black Fungi.*—Here are found a large and varied group of fungi which include both parasitic and saprophytic species. Their mycelium is often hard and compact and is characteristically dark in color. The ascocarp consists of a very small, flask-shaped structure, the *perithecium*, lined with

a hymenium and opening to the air by a minute pore. Here belong the knot and wart fungi found on so many woody plants, many of which, such as the "black knot" of plums (Fig. 170), are serious parasites. In this order also occur the destructive chestnut bark fungus and other important disease-producing organisms.

3. *Perisporiales or Mildews.*—These small fungi produce a cobweb-like mycelium which spreads over the surface of the

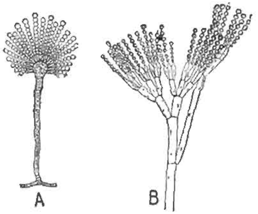


FIG. 171.—*Aspergillus* (*A*) and *Penicillium* (*B*). Hyphae bearing chains of air-spores or conidia. (*From Strasburger*).

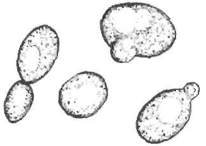


FIG. 172.—Yeast (*Saccharomyces*). Single-celled plants in various stages of division by budding.

leaves of many plants and is parasitic on their epidermal cells. Conidia are produced in abundance. Toward the end of the season, as the result of a sexual union between female branches (ascogonia) and antheridia, there are developed a host of minute, dark, globular, and hard-walled ascocarps or perithecia. These are filled with asci, and on breaking open the next spring, release the ascospores.

4. *Plectascales or Blue and Green Molds* (Fig. 171).—Here are found the common molds (aside from the Mucorales) which appear on bread, cheese, leather, and almost all organic substances which will "mold" when subjected to dampness. Their abundant masses of conidia are typically greenish or bluish in color. Small, rounded ascocarps, full of irregularly scattered asci and lacking a hymenium, are occasionally produced. No members of the order are parasitic, but a species of *Penicillium* is of economic importance as responsible for the peculiar flavor of Roquefort cheese.

5. *Saccharomycetes or Yeasts* (Fig. 172).—These minute plants are usually included within the ascomycetes. The individual is a

single cell, possessing a definite nucleus, cytoplasm, and sap-cavity *and producing, by the process of "budding", a loose, irregular* chain of cells. When conditions become unfavorable, the contents of some of the cells divides into four spores, forming a structure which is thought to represent a modified ascus. The yeasts are saprophytes on sugary substances, thriving in the absence of free oxygen, and are the chief agents in alcoholic fermentation, a process which has been described in a preceding chapter. Their use in the raising of bread is familiar to everyone.

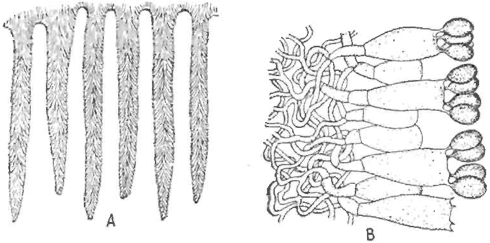


Fig. 173.—Spore production in a basidiomycete. *A*, cross section of a few of the gills of a mushroom. *B*, a portion of the surface of one of the gills, much enlarged. The stout cells are basidia. Each of them bears four basidiospores on *slender stalks or sterigmata. The lowest basidium has shed its spores.*

Basidiomycetes or Basidia Fungi.—Like the Ascomycetes, this is a very large and varied group containing over 20,000 species. Its specialized reproductive structure, the *basidium* (Fig. 173), is the swollen terminal cell of a hypha and typically bears four *basidiospores*, each supported on a delicate stalk or *sterigma* (plural *sterigmata*). The basidia are arranged in a more or less definite hymenium. Aside from this difference in the method of spore production, the group as a whole is distinguished from the Ascomycetes by the almost complete absence of sexual processes and by the larger and more conspicuous fruiting bodies. The Basidiomycetes are regarded as the highest of the fungi and are believed to have come from Ascomycetes, the basidium representing a much modified ascus.

A few orders, notably the Smuts (*Ustilaginales*) and the Rusts (*Uredinales*) differ from the typical Basidiomycetes (or *Autobasidiomycetes*) in having basidia, or structures thought to repre-

sent basidia, which instead of being one-celled are composed of three or four cells, each producing a spore.

1. *Ustilaginales or Smuts.*—Here are found a number of destructive parasites which attack floral organs, especially among members of the Grass family. The mycelium spreads through the body of the host plant and at flowering time gathers in dense masses, particularly in the ovaries and surrounding tissues, which become swollen and distorted, and form the so-called smut. The mycelium here becomes transformed directly into a mass of black, thick-walled spores which survive the winter. On germinating the next spring, each spore produces a short filament of three or four cells, the *promycelium*. This promycelium is thought to represent a basidium, for each cell bears one or more spores or *sporidia*, which are capable of infecting new plants. The smuts of corn, oats, and wheat are particularly destructive.

2. *Uredinales or Rusts.*—All members of this order are parasites, often becoming very destructive, and have the most complicated life histories of any of the fungi.

The common wheat rust, *Puccinia graminis* (Fig. 174), is the best known member of the group. The mycelium of this species, in the tissues of the wheat plant, breaks through the surface and produces clusters of one-celled, reddish, rough-walled spores, the summer spores or *uredospores*, which give a rust-like appearance to the stems and leaves. Each uredospore may germinate directly on another wheat plant and produce a new mycelium. Toward the end of the season, clusters of another type of spore are produced at the surface of the plant. These are black, two-celled and heavy-walled, and are known as winter spores or *teleutospores*. They live over the winter and in the following spring each cell germinates into a slender, four-celled, saprophytic promycelium somewhat as in the smuts. Each of the cells here produces but a single sporidium, however, so that the structure displays a much closer resemblance to a typical basidium. The remarkable fact has been demonstrated that these sporidia (or basidiospores) do not infect wheat, but will attack only plants of the barberry. The spores germinate on the barberry leaves, penetrate the tissues, and produce there a vigorous mycelium. On the upper surface of the leaf soon appear small flask-shaped structures, the *spermagonia*, which produce enormous numbers of very minute cells or *spermatia*. As its name implies, this organ has been thought to represent the male sexual appa-

ratus. Whatever its original share in the life cycle may have been, however, it seems now to be entirely functionless. On the lower surface of the barberry leaves are formed cluster-cups or

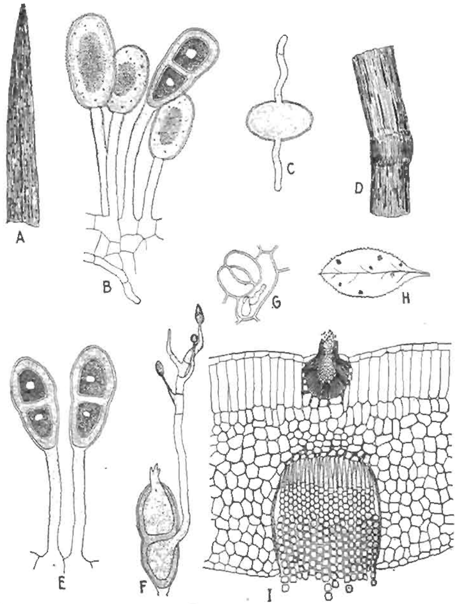


FIG. 174.—*Puccinia graminis*, the wheat rust. *A*, wheat leaf with groups of summer spores (uredospores). *B*, uredospores (one teleutospore among them). *C*, germinating uredospore. *D*, wheat stem with masses of winter spores (teleutospores). *E*, two teleutospores. *F*, germinating teleutospore, producing a promycelium on which are borne the sporidia. *G*, sporidium germinating on epidermis of barberry leaf. *H*, lower surface of barberry leaf, showing cluster-cups or aecidia. *I*, section through the leaf of barberry showing spermagonium on upper surface and aecidium on lower. The aecidium is producing masses of aecidiospores, which infect wheat plants. (*B, C, F and G after De Bary*).

aecidia (singular, *aecidium*), flaring, cup-shaped structures from the base of which arise long rows of *aecidiospores*. These, in

turn, never reinfect barberry but attack only wheat plants, thus completing the life cycle.

Many other rusts resemble this species in alternating between two distinct hosts, but some are confined entirely to one. The rusts produce many serious plant diseases, among them the white

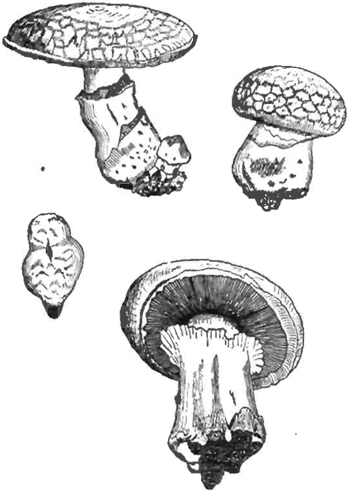


FIG. 175.—*Agaricus campestris*, the common mushroom. Views of young and of mature fructifications. The broad, expanded cap or *pileus* bears the gills on its lower surface and is supported by the stalk or *stipe*. The young fructification, at left, is surrounded by a membrane or *volva*, which breaks as the pileus expands, and the remains of which can be seen as a ring around the stipe.

pine blister rust, which has its uredo-stage on currants and gooseberries; the apple rust, which has its teleuto-stage on red cedar, and many others.

The typical or true Basidiomycetes, or *Autobasidiomycetes*, include two main sub-classes; the *Hymenomycetes*, in which the fruiting surface or hymenium is exposed to the air, and the *Gasteromycetes*, in which it is enclosed within the tissue of the

fructification. These are both chiefly saprophytic, the extensive *mycelium penetrating deeply and under favorable conditions* producing at the surface very characteristic fructifications or *sporophores*.

A. *Hymenomycetes*.—These fungi are divided into a number of orders, but by far the most important are the *Agaricales* or agarics, which include the mushrooms and toadstools. This is a

FIG. 176.—A gill fungus growing in a hollow tree. The mycelium penetrates the wood in all directions and has produced the fruiting body here shown. In cases like this it is sometimes hard to tell whether the fungus is a parasite or a saprophyte.

very large group and includes the most important of the so-called "fleshy fungi". Because of the edibility of the sporophore of many of its members and the poisonous character of a few of them, the Agaricales have received intensive study and are perhaps more widely known than any other fungi.

The order is divided into a number of families according to the type of fruiting body produced. In the Agaricaceae or gill fungi (Figs. 175, 176, and 5) which are the mushrooms and toadstools proper, the hymenium covers the surface of plate-like structures or *gills*. The sporophore in this group is the typical "toadstool", which consists of a stalk or *stipe* supporting a broad

cap or *pileus*, from the under surface of which hang the gills. A few of the species are regularly cultivated and constitute a food product of some importance. A number are also poisonous, and

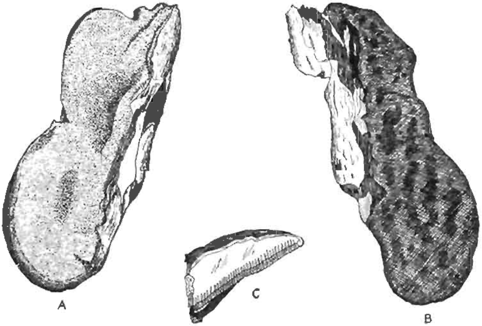


FIG. 177.—A pore fungus. Bracket-like fructification of one of the specie which grows on tree-trunks. *A*, lower surface, showing pore openings. *B*, upper surface. *C*, section through a part of the fructification, showing the long, tube-like pores, on the inner surfaces of which the spores are borne. This type of fructification adds a new layer each year, and two such annual layers are here evident.

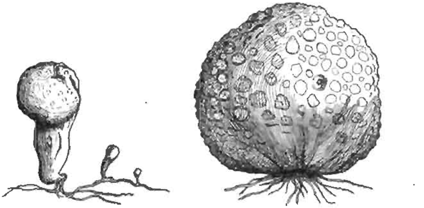


FIG. 178.—Puff-balls General appearance of young and of mature fructifications.

the amateur mushroom collector is always in danger of adding them to his menu. In the polypores (Polyporaceae, Fig. 177) the hymenium lines narrow tubes which open by pores on the surface of the pileus. These include many mushroom-like types as well

as the hard, bracket-like forms so common on rotting logs, which are very destructive of wood and are sometimes parasites upon living trees. In the Tooth fungi (Hydnaceae) the hymenium *covers the surface of tooth-like or spine-like projections.*

Close to the Agaricales are the Coral fungi (*Clavariales*, Fig. 179) the much-branched sporophores of which are covered by the hymenium.

B. *Gasteromycetes.*—These are the highest of the fungi. Their fructification is in general a rounded mass of hyphae, the outer-

FIG. 179.—Saprophytic fungi. Coral fungi, above, and young puff-balls, below. In the photograph are also ferns, lycopods, and leafy liverworts.

most layer of which becomes differentiated into a cortex or *peridium*, surrounding the inner mass of hyphae and basidia which is called the *gleba*. Two important orders are the *Lycoperdales* and the *Phallales*.

1. *Lycoperdales or Puffballs* (Figs. 178 and 179).—The sporophore is here a globular structure which often becomes very large and is usually edible when young. At maturity the peridium breaks open at the top and a mass of dark spores is discharged therefrom.

2. *Phallales or Stink-horns* (Fig. 180).—The gleba here ripens into a foul-smelling mass, breaks through the peridium, and is

pushed upward at the end of a stalk. The rank odor attracts to these fungi many carrion-loving insects.

Lichens.—In addition to the algae and fungi, the thallophytes include a remarkable group of composite plants, the *lichens*. These are fungi in the mycelium of which groups of algal cells are entangled (Fig. 181). The advantage to the fungus of this intimate association is evident, and the alga is also probably benefited to some extent. Instead of regarding this as a case of true symbiosis, however, most botanists look upon the fungus as parasitic on the algal member of the combination, even though this parasitism is very mild. The two component plants have been artificially separated, and it has been found that the alga can exist independently in every case but that the fungus is unable to do so. Lichens have also been "synthesized" experimentally by bringing appropriate algae and fungi together. The fungus members of lichens are almost always ascomycetes. A number of different algae are represented in lichens but these belong mainly to the Cyanophyceae and to the Protococcales. All are very simple in character. The fungus mycelium is often somewhat gelatinous and thus tends to absorb water readily and hold it tenaciously. It is much more compact, differentiated, and definite in shape than that of ordinary fungi and is essentially a flat thallus (Fig. 182). Three main types of thallus are recognized: The *crustaceous*, which grows closely appressed to the surface of rocks, bark and similar structures; the *foliose*, in which the thallus is broader and somewhat branched, suggesting that of the liverworts; and the *fruticose*, in which it is slender and very much branched and may either be erect or hanging.

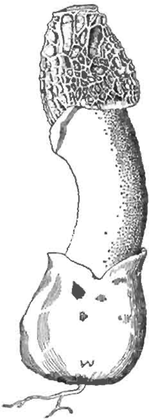


FIG. 180.—*Phallus*, the stink-horn. Fructification, showing the gleba, *above at the end* of the stalk, and the remains of the peridium below.

Asexual multiplication is accomplished by the production and dispersal of *soredia* or small bits of mycelium in which a few algal cells are entangled. The fructifications are conspicuous, and the

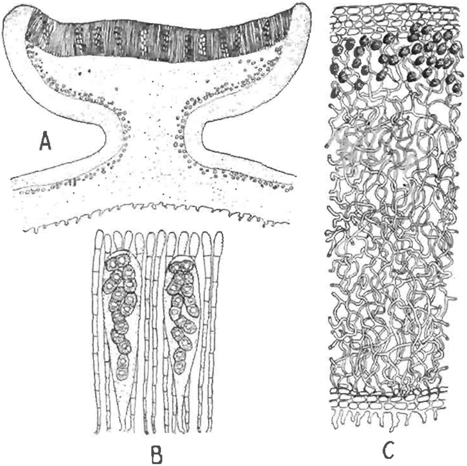


FIG. 181.—*Physcia stellaris*, a lichen. *A*, section through an ascocarp, showing fruiting-surface (hymenium) of asci and sterile hairs. *B*, a portion of the hymenium enlarged, showing two asci and several paraphyses. *C*, section through the thallus, showing the mass of mycelial filaments and (near upper surface) a group of algal cells embedded in the mycelium.

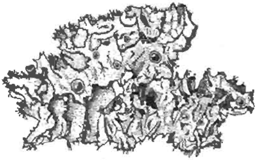


FIG. 182.—A lichen (*Parmelia*), showing the rather thin and thallus-like character of the plant body and the cup-shaped sac-fruits or ascocarps.

ascocarps are usually either cup-shaped or disc-shaped, as in the Discomycetes (Fig. 181). Definite and functional sex organs, somewhat suggestive of those in the red algae, have been demonstrated in certain species.

Lichens are usually xerophytic and will thrive on bare rocks and exposed places where no other vegetation can exist. Their importance in the economy of nature is therefore considerable, but they include only a few species which are of direct practical value to man.

QUESTIONS FOR THOUGHT AND DISCUSSION

669. The thallophytes are the most varied of all the four main divisions of the plant kingdom. Can you suggest why this is so?

670. In what way is the classification of the thallophytes given in this book an "artificial" one?

671. All the groups of algae are found in the ocean, but few in fresh water. Explain.

672. Of what advantage is the possession of motility to the zoöspores of the algae?

673. Zoöspores of algae will generally swim toward the light rather than away from it. Of what advantage is this to the plant?

674. Unicellular algae are frequently spherical in form, but among larger types the body is never a solid sphere. Explain.

675. Algae are in general much more filamentous and finely branched than land plants. Explain.

676. Algae which are completely and somewhat deeply submersed all the time are much more finely branched and dissected than those which are near the surface or are partially exposed to the air for some of the time. Explain.

677. Are algae commoner on a rocky coast or on a sandy one? Explain.

678. Seaweeds which grow between tide marks are often very gelatinous. Explain.

679. The "plankton" is more abundant in the cooler parts of the ocean than in the warmer ones. Why?

680. The largest of the algae are usually found in cool northern seas rather than in the warm tropical ones. Why?

681. There are no living algae or other green plants at depths greater than a few hundred feet below the surface of the ocean. Why?

682. What factors may affect the depth to which algae will grow in the ocean?

683. Since no green plants live in the deeper portions of the ocean, how is it possible for fish and other animals to live there?

684. What is the ultimate source of the food of fishes which live near the surface of the ocean, in the open sea?

685. Why are very shallow parts of the ocean, like the Grand Banks of Newfoundland and the North Sea, such great fishing grounds?

686. The algal flora near shore, and especially near mouths of large rivers, is apt to be very rich. Explain.

687. What great element of the food supply of man has its source in the algae?

688. Blue-green algae can thrive in relatively dry places as compared with other algae. What structural peculiarity of theirs makes this possible?

689. Blue-green algae are generally found in waters which are rich in organic matter. What does this suggest as to differences between their methods of nutrition and those of ordinary green plants?

690. Blue-green algae can thrive in hot springs and in warmer waters generally than can most of the other algae. Can you suggest a reason for this?

691. What do we mean by saying that one group of plants is "on the direct line of ascent" to another?

692. Why is it believed that the green algae rather than the other algal groups are on the direct line of ascent to the bryophytes?

693. What are the advantages and the disadvantages of the coenocytic condition?

694. Brown seaweeds in general have a much thicker and tougher plant body than the rest of the algae. Explain.

695. What are the advantages conferred by the possession of bladder-like floats in the brown algae?

696. In what important particular is fertilization in *Fucus* different from that in any other alga described in the text?

697. Which of the other algae do the red algae most resemble in their reproductive structures?

698. What makes us believe that the fungi have come from the algae rather than the algae from the fungi?

699. There are many more species of fungi than of algae. Explain.

700. Which are larger plants, on the whole, the fungi or the algae. Why?

701. Why do you think it is that most fungi inhabit the land and most algae the water?

702. Is wind or water the commoner agency for the distribution of the spores of the algae? of the fungi?

703. Why are so many fungi edible, but so few algae?

704. Why are fungi so much more important economically than algae?

705. Through what steps do you think that the parasitic habit in fungi may have arisen?

706. Spores of a given species of parasitic fungus will generally germinate and grow only on one or at most a few host plants. Is there anything analogous to this "discriminating power" in any of the other physiological activities of plants?

707. Why are the fungous diseases of plants so much more common in the United States now than they were two hundred years ago?

708. Why is a wound much more liable to attack by fungi than is a healthy area?

709. Why are the fungous diseases usually more prevalent in wet seasons than in dry?

710. Why is a spray of such a substance as copper sulphate effective in preventing fungus attacks on plants?

711. How do you explain the fact that a piece of moist bread shut up in a box will almost always develop mold?

712. Why do you think it is that the bacteria are the commonest disease-producing parasites in animals, but that the higher fungi are the most important causes of disease among plants?

713. From an agricultural point of view, what various means can you suggest for combatting the attacks of the fungous diseases of crop plants?

714. What evidence is there that bacteria are plants rather than animals?

715. The minute size of bacteria is thought to be one reason why they are able to maintain such a very high degree of physiological activity. Why?

716. Why cannot plants well be treated with serums and vaccines, as can animals?

717. In killing bacteria in liquids by heat, it has been found that several boilings, each followed by cooling to ordinary temperature, are much more effective than one long boiling. Can you suggest a reason for this?

718. Algae themselves are not harmful in drinking water but their abundance there is often a sign that such water may be dangerous to drink. Why?

719. Why is it desirable to boil surgical instruments before using them to perform an operation?

720. Why are coughing and sneezing particularly dangerous as means of spreading infection?

721. Pasteur found that a sample of air taken in Paris contained many bacteria but that one taken in the high Alps was free from these organisms. Explain.

722. Can you think of any reason, aside from their invigorating climate, which should make a mountainous or arctic region particularly healthful?

723. Why will food keep longer in "cold storage" than under ordinary conditions?

724. Why do not dried vegetables and meats decay?

725. Name at least five different methods which are employed to preserve food and keep it from decaying, and state what makes each method effective.

726. What group of algae does *Rhizopus* most resemble in its reproduction?

727. What forms among the algae do the Mucorales resemble in having plants which look alike but are entirely different sexually?

728. Some kinds of fungi, notable the truffles, grow only around certain species of forest trees. What explanation for this fact can you suggest?

729. Teleutospores are thicker-walled than uredospores. Explain.

730. Can you suggest why it is that fleshy fungi are often so good to eat?

731. What conditions favor a luxuriant growth of mushrooms and toadstools?

732. Of what advantage to the fungus is the production of the "toadstool" type of fruiting body?

733. What are the advantages of the gills, pores, and teeth commonly present in the fruiting bodies of the fleshy fungi?

734. What is the advantage of the "bracket" form of fruiting body?

735. Of what use to the stink-horn fungus is its carrion-like odor?

736. In general, what insects do you think are the commonest carriers of fungus spores? Why?

737. In a lichen plant, what is the advantage gained by the fungus and what by the alga?

738. "Slavery" is the term sometimes used to describe the relation of alga to fungus in the lichen plant. Why is "slavery" perhaps a better term than "symbiosis" or "parasitism"?

739. How different in general is the substratum on which lichens grow from that which supports algae or fungi?

740. Lichens particularly like rough surfaces to grow on. Explain.

741. Since algae and fungi are both usually best developed in a moist environment, how does it happen that lichens will often thrive in dry situations?

742. Lichens are greener when moist than when dry. Explain.

743. The vegetative body of a lichen is more thin and thallus-like than that of most fungi. Explain.

744. Aside from their small size, why do you think it is that the algal members of most lichens are either Cyanophyceae or Protococcales?

745. What conditions must be present before an ascospore produced by a lichen plant can give rise to a new lichen plant?

746. Of what importance are lichens in nature?

747. What other instances do you know of, aside from lichens, where fungi become intimately associated with green plants?

REFERENCE PROBLEMS

117. Name some algae which are of economic importance.

118. What is "diatomaceous earth" and how was it produced?

119. Give an example of a change in some agricultural practice which has come about since the existence and importance of bacteria have become recognized.

120. What is "Pasteurization" and how is it useful?

121. Species of bacteria which look alike may often be distinguished from one another by differences in their physiological activity. What examples can you cite from the seed plants of the use of physiological differences to distinguish two plant varieties which look very similar?

122. What is the life history of the white pine blister rust and what is a good means for combatting this fungus?

123. What are fungus galls and how are they produced?

124. What are "fairy rings" and how do you explain them?

125. How are truffles gathered?

126. What parasitic animals are there whose life history is somewhat analogous to that of the rusts?

127. Who first discovered that lichens are composed of algae and fungi?

128. What lichens are of economic importance?

129. Give the derivations of the following terms and explain why each is appropriate:

Heterocyst	Pyrenoid	Basidium
Zoöspore	Plankton	Perithecium
Zygospore	Trichogyne	Hymenium
Oöspore	Mycelium	Sterigma
Heterogamy	Toxin	Teleutospore
Antheridium	Conidium	Uredospore
Oögonium	Ascus	Aecidium
	Soredium	

CHAPTER XV

THE BRYOPHYTA

The second of the four great divisions of the plant kingdom is the *Bryophyta* or bryophytes, the members of which we know commonly as the liverworts and mosses. This group is much smaller than the thallophytes, containing only about 16,000 species, nor does it approach them in the diversity of plant types which it displays. All of its members are lowly and inconspicuous, the tallest mosses rarely attaining a decimeter in height. From the economic point of view the group is of very minor consequence. To the botanist, however, the bryophytes are of particular interest in helping to picture for us those ancient plants which first crept out of the sea to invade the dry land, and which therefore took the first steps along the evolutionary road leading up to our dominant and familiar seed plants.

The bryophytes are undoubtedly a very ancient group and their history is necessarily obscure. We have good reason to believe, however, that they arose from plants resembling some of our higher algae of today, and several connecting links between algae and liverworts have accordingly been suggested. The two main characteristics which distinguish the bryophytes as a whole from these ancestral thallophytes are the establishment of a clearly marked alternation of generations and the possession of multicellular sexual organs.

Alternation of Generations.—As outlined in a previous chapter, these plants possess a definite sexual gamete-producing member, the *gametophyte*, which is followed in the life history by an equally definite non-sexual, spore-producing member, the *sporophyte*. The sporophyte here is little more than a spore case and is always attached to the tissues of the gametophyte, never becoming an independent individual as it does among the ferns and their allies. The beginnings of this alternation of generations, as we have seen, make their appearance here and there among the thallophytes, but when we reach the liverworts and mosses it becomes regularly established and is henceforth a distinctive feature in the life histories of all species throughout the plant kingdom.

Multicellular Sexual Organs.—The sexual organs of the bryophytes have also attained a degree of complexity far above those of the thallophytes. In the latter group, with a few minor exceptions, the structures which produce the eggs and the sperm are modified single cells, the gametes being formed directly out of the cell contents. In the bryophytes, however, the gamete-producing organ has a definite, many-celled wall surrounding the

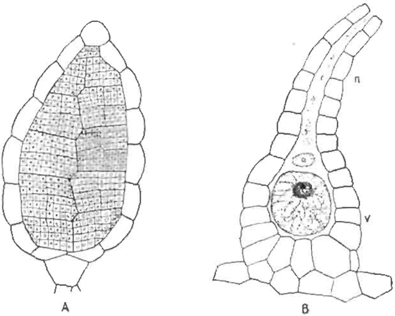


FIG. 183.—Multicellular sexual organs of a bryophyte (*Ricciocarpus*). *A*, antheridium. *B*, archegonium. *v*, venter. *n*, neck. A large egg is evident in the venter, but the ventral canal cell and neck-canal cells are largely broken down, following the opening of the neck of the archegonium. See also Figs. 185 and 196.

cell or group of cells which develop into the gametes (Fig. 183). The female sex organ is now known as the *archegonium*. It is a somewhat flask-shaped structure, the swollen lower portion of which is known as the *venter* and the elongated upper portion as the *neck*. The wall is a single cell-layer in thickness. Most of the cavity of the venter is occupied by a large egg-cell, and just above this lies a much smaller *ventral canal cell*. Filling the neck are a row of narrow *neck-canal cells*. When wet, the neck opens, the neck-canal cells break down, and a sperm enters to fertilize the egg. The male sex organ is still known as the *antheridium*. In bryophytes it has typically a short stalk and is somewhat elongated. Its wall, one cell-layer in thickness, surrounds a mass of small, squarish cells within each of which a motile sperm is developed, provided with two cilia. When wet, the antheridium

breaks open and liberates the sperms, which swim about and under favorable conditions enter archegonia and effect fertilization. Archegonia and antheridia, or structures which have been derived from them, may be recognized in the gametophytes of all the remaining members of the plant kingdom.

Bryophytes are divided into two classes, the *Hepaticae* and the *Musci*.

Hepaticae or Liverworts.—The members of this class are low-growing plants, chiefly inhabiting moist places. Their vegeta-

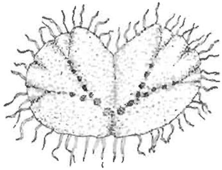


FIG. 184.—*Ricciocarpus*, a simple, floating liverwort. The round bodies lying at the bottoms of the furrows on its surface are sporophytes, each of which has arisen there from a fertilized egg in an archegonium. On the lower surface of the thallus are groups of thread-like absorbing organs or *rhizoids*.

tive body is a flattish thallus which creeps over the surface of the ground, and is attached thereto by thread-like filaments or *rhizoids*. In some types it is cut up into leaf-like lobes. Here are found the lowest and most alga-like of the bryophytes. They are commonly divided into the *Marchantiales*, *Jungermanniales*, and *Anthocerotales*.

1. *Marchantiales*.—The thallus of these plants is a thick, dichotomously forking structure, in the upper or dorsal portion of which occur air spaces or chambers, communicating directly with the outside and thus freely exposing to the air the delicate chlorophyll-bearing cells of the interior. In *Riccia* and its allies (Fig. 184), the simplest members of the order, the archegonia and antheridia (Figs. 183 and 185) occur along grooves in the upper portion of the thallus and are sunken just below its surface. The sporophyte (Fig. 185) which develops from the fertilized egg is nothing more than a spore case or sporangium, often called among bryophytes the *sporogonium*, and here consists merely of a mass of spores surrounded by a definite wall. These spores, like all produced by sporophytes, occur in *tetrads* or groups of four.

The sporogonium is sunken in the tissues of the thallus, to which it is attached at the base and from which it draws its food. In the higher members of the order, as illustrated by the common

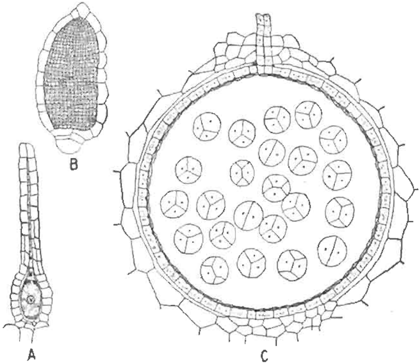


FIG. 185.—*Ricciocarpus natans*. *A*, archegonium. × 200. *B*, antheridium. × 150. *C*, sporophyte, contained within the remains of the archegonium, and with a thin wall of its own. The spores are borne in groups of four. × 100.

FIG. 186.—*Marchantia*. Thallus bearing female receptacles, in which occur the archegonia. A single male or antheridial receptacle is shown separately.

genus *Marchantia* (Fig. 186), the sexual organs are borne on specialized discs, each carried up above the surface of the thallus by a stalk. The sexes are separate here, some gametophytes

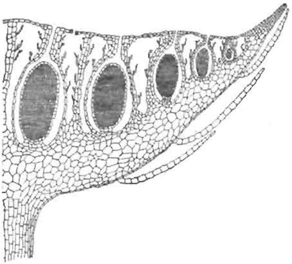


FIG. 187.—*Marchantia.* Section through the male receptacle, showing the antheridia sunken below the surface.

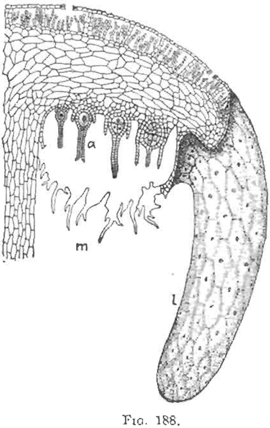


FIG. 188.

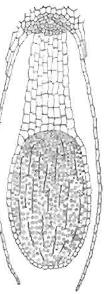


FIG. 189

FIG. 188.—*Marchantia.* Section through female receptacle. *a*, archegonia, two at left unfertilized, two at right with young sporophytes. *m*, membranous fringe. *l*, finger-like lobe.

FIG. 189.—*Marchantia.* Sporophyte, developed from a fertilized egg. The enlarged capsule contains spores and elaters. It is supported by a stalk or seta, which is embedded in the tissues of the gametophyte by a foot. × 45.

bearing only antheridia (Fig. 187) and some only archegonia (Fig. 188). The sporophyte (Fig. 189) is more specialized than that of *Riccia* for it includes not only a spore case but a short stalk or *seta* the growth of which carries the spore case out and away from the thallus. The base of this seta is enlarged into a *foot*, anchoring the sporophyte in the tissue of the thallus and absorbing food therefrom. Furthermore, not all of the central portion of the sporogonium itself produces spores, for many of the

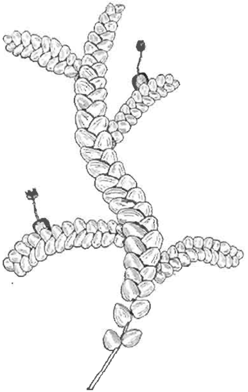


FIG. 190.—*Porella*. Portion of thallus, showing the two rows of leaves. One of the two capsules figured has opened and liberated its spores.

cells grow instead into long, spirally thickened elements, the *elaters*, which assist in loosening and scattering the spore mass at maturity. The relative amount of sporophyte tissue which does not contribute directly to the production of spores, and is therefore called *sterile* tissue, increases steadily as we trace the upward evolution of the sporophyte. In the simplest case (among certain thallophytes), the fertilized egg develops into a group of spores. In *Riccia*, the only sterile tissue is the sporangium wall; in *Marchantia*, the seta and foot are added; in the mosses still other regions are "sterilized", and in the higher plants the spores them-

selves constitute but a very small portion of the sporophyte as a whole.

2. *Jungermanniales or Leafy Liverworts.*—In number of species this order is by far the largest of the three groups of liverworts. Its thallus is much less complex internally than that of the Marchantiales. Externally, however, it is more specialized, for in most species it is divided into a slender axis

FIG. 191.—*Anthoceros.* Portion of thallus, showing several sporophytes, one of which is splitting open and liberating the spores.

or stem and three crowded rows of small and delicate lobes or "leaves" (Fig. 190). The stem never rises to an erect position but is always prostrate on the ground, to which it is attached by *rhizoids.* Sex organs are borne on the main axis or on short lateral branches. The sporophyte develops a much longer seta than in the Marchantiales and the spore case contains still more sterile tissue. At maturity it breaks open into four spreading lobes.

3. *Anthocerotales.*—The gametophyte in this group is a simple, flat thallus (Fig. 191), but the sporophyte is remarkable in several particulars. In the genus *Anthoceros,* the best known member of the order, the sporophyte (Fig. 192) is long and slender and is

well anchored in the thallus by its foot. Just above the foot is a growing region, through the activity of which the sporophyte continues to elongate during the whole season. The spores at

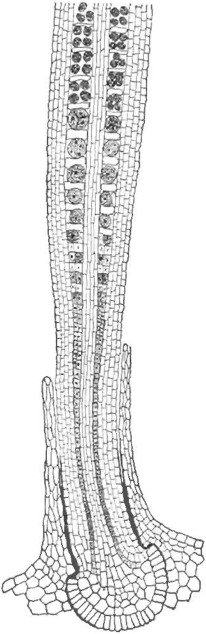


FIG. 192.—The sporophyte of *Anthoceros*. Longitudinal section of basal portion, showing the large *foot*, embedded in the gametophyte. The spore-bearing tissue surrounds the sterile *columella* within, and is surrounded by a layer of sterile, chlorophyll-bearing tissue without. The base of the sporophyte continues to grow, adding progressively to these various tissues.

the tip ripen first, and ripening proceeds slowly downward, the spore-case gradually splitting into halves (Fig. 191). Its internal

structure is more highly differentiated than in any other of the bryophytes. A core of sterile tissue, the *columella*, occupies the center or axis. Around this is a layer of spores, which in many species is broken up by groups of sterile cells. The wall outside this is three or four cell layers in thickness, and except for the outermost one, or epidermis, its cells are provided with chlorophyll and are often separated somewhat by intercellular air spaces. Well developed stomata, with guard cells much like those in the higher plants, occur in the epidermis. The sporophyte of the Anthocerotales is therefore able to carry on photosynthesis actively, though it still necessarily depends upon the gametophyte for water and mineral salts. This group has always been of particular interest to botanists as suggesting a possible connection between the bryophytes and those higher plants in which the sporophyte is an independent individual.

Musci or Mosses.—The mosses are much commoner and more familiar plants than the liverworts, and under certain conditions form an important element in the vegetation. Many of them thrive only in moist situations but others are common on ordinary dry soil and still others live under exceptionally xerophytic conditions where few plants can grow. The moss-plant is typically erect and consists of a stalk around which small, delicate leaves are arranged in spirals. The stem has very little internal differentiation and the leaves are only one or two cells in thickness, so that the vegetative organs are far from approaching in complexity those of ferns and seed plants. As in the liverworts, the plant is attached to the soil by thread-like rhizoids. The sporophyte also shows an advance over earlier conditions in a progressive increase in sterile tissue, particularly in the higher forms; and in opening by a distinct lid, or *operculum*, at the top.

Two main orders are recognized, the *Sphagnales* and the *Bryales*.

1. *Sphagnales or Peat Mosses.*—These all belong to the single large genus *Sphagnum*, characteristic of the bogs and swampy regions of temperate climates. The spore germinates into a flat, thallus-like structure from the surface of which arise upright and much-branched shoots, thickly covered with small leaves (Fig. 193). Many of the leaf cells are dead and empty and are so constructed that they will absorb and hold large quantities of water. At the tips of the main branches are borne the sexual organs. The globular capsule is provided with a well-developed

foot, its wall is thick, and much of the central tissue is sterile, the spores occurring in a rather small, dome-shaped mass in the upper portion. There is no true seta but the sporophyte is carried upward on a stalk formed by the gametophyte.

FIG. 193.—*Sphagnum*. Leafy shoot of the gametophyte, with three capsules at the top.

2. *Bryales or True Mosses.*—These are the common mosses, numbering over 12,000 species and widely distributed over the globe. Many of them are particularly well suited to live in cold or dry situations and they often form the vanguard of an advancing vegetation.

The spore does not germinate directly into what we know as a moss plant, but produces instead a mass of green filaments, the *protonema* (Fig. 194). From this arise erect branches which grow into the leafy shoots with which we are familiar (Figs. 6 and 195). The stem is usually but a few centimeters in height and shows little complexity, although there may often be distinguished a firm central mass of tissue—presumably the region of conduction—and a softer zone outside. Nothing approaching the highly differentiated stem structure of ferns and seed plants

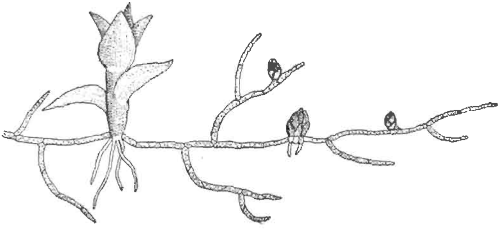


FIG. 194.—Moss protonema, the delicate, thread-like structure which grows from the germinated moss spore. Along this protonema several young moss plants are arising, the one at the left well started, the other three more buds.

is present, however. The leaves are typically small and narrow, and but one layer of cells in thickness. They may often become

very dry and still retain their vitality. The filaments of protonema, to which the moss plant still remains attached, continue to grow and serve as a means for anchorage, absorption, and dispersal.

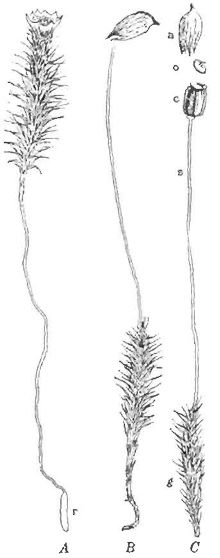


Fig. 195.

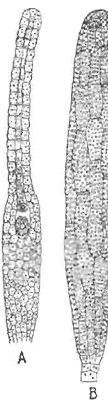


Fig. 196.

Fig. 195.—A moss (*Polytrichum commune*, the hair-cap moss). *A*, male plant which bears antheridia at its tip. *B*, female plant, showing mature sporophyte. *C*, female plant with its various portions separated. *g*, gametophyte or moss plant. *s*, seta or stalk. c, capsule. *o*, operculum. *a*, calyptra. (*From Gager's "Fundamentals of Botany", P. Blakiston's Son and Co., Philadelphia*).

Fig. 196.—Sexual organs of a moss (*Mnium*). *A*, archegonium (in section). *B*, antheridium. × 100.

Sexual organs (*Fig. 196*) are borne at the tips of the branches, sometimes on the same plant but often on separate individuals. The sporophyte usually develops a long seta, the growth of which carries the capsule far up above the moss plant. Remains of

the archegonium are carried up with it and form a protecting cap or *calyptra* which covers the young capsule. The capsule itself (Fig. 197) possesses a central columella and much other sterile tissue, so that the spore-bearing layer, which surrounds the columella, is relatively thin. The operculum drops off at

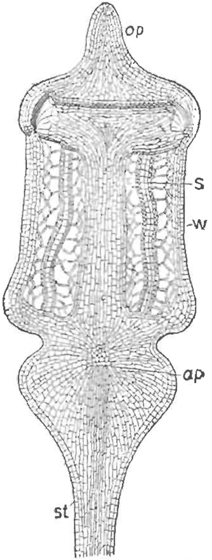


FIG. 197.—Longitudinal section through the capsule of a moss (*Polytrichum*). *st*, seta. *ap*, apophysis. *w*, wall. *c*, columella. *s*, spore-sac, surrounded on both sides by loose tissue. (*From Goebel*)

maturity and the liberation of the spores is controlled by a ring of teeth projecting inward from the edge of the wall. Just below the capsule there is typically an enlarged region, the *apophysis*, which is often brightly colored and may sometimes possess chlorophyll. The capsule is very diverse in size, shape, and structure throughout the whole group.

Fertilization is probably effected rather rarely, owing to the fact that an abundance of water is necessary in which the sperms may swim about. Perhaps as a result of this we find many devices among the mosses by which asexual reproduction is effected, and most of the new individuals produced probably arise by this means.

Despite its large size and relatively high specialization, the mosses are not believed to have led directly to any of the higher plant groups, but we look instead to such simpler forms as *Anthoceros* for a suggestion as to how the great gap which now exists between bryophytes and pteridophytes may have been bridged.

QUESTIONS FOR THOUGHT AND DISCUSSION

748. What great change in the character of the spores occurs as we pass from algae to bryophytes?

749. What is the advantage of a multicellular sexual organ over the primitive unicellular type?

750. What reason can you suggest for the presence of the ventral canal cells and the neck-canal cells in the archegonium?

751. What exceptions are there to the general rule that the thallophytes have unicellular sexual organs?

752. Where else in the plant kingdom below the liverworts have we found dichotomous branching? Do you think that it is primitive or not? How does it differ from the typical branching of the higher plants?

753. Of what advantage to the moss plant is the seta?

754. Why do you think it is that the bryophytes have never been able to produce plants of any great height?

755. In bryophytes, what are the advantages and the disadvantages of the thallus type and of the leafy type of plant?

756. In the general character of their thallus, what group of algae do the liverworts most resemble?

757. Why do you think it is that the liverworts are largely confined to moist places, while the mosses often thrive in relatively dry ones?

758. What notable resemblance is there in structure between the thallus of the liverworts and the leaves of the higher plants?

759. What are the advantages of the system of air chambers in the thallus of the Marchantiales?

760. Enumerate the various ways in which the Anthocerotales are closer to the higher plants than are the rest of the bryophytes.

761. Name all the ways you can think of in which the sporophyte of *Anthoceros* resembles, and differs from, that of the seed plants.

762. The shoots of *Sphagnum* are greenish or grayish-green instead of dark green as in most mosses. Why?

763. Why is *sphagnum* (the dead and dried remains of *Sphagnum* plants) a very good absorbent?

764. What important part in the economy of nature is played by the mosses?

765. What does a moss protonema resemble, and what does its presence suggest as to the ancestry of the mosses?

766. Bryophytes are generally very tolerant of shade. Explain.

767. Where at present on the earth is vegetation "headed by a vanguard of mosses"?

768. From your study of the bryophytes (and of other plant groups) do you think that all parts of the plant change at the same rate during the progress of evolution? Explain and illustrate.

REFERENCE PROBLEMS

130. Where does peat come from and how has it been formed?

131. Why is *sphagnum* so much used for surgical dressings?

132. Give the derivation of the following terms and explain in what way each is appropriate:

Archegonium	Columella	Hypophysis
Elater	Operculum	Protonema
	Calyptra	

CHAPTER XVI

THE PTERIDOPHYTA

In passing from the bryophytes to the pteridophytes, which include the ferns, club mosses, and horsetails, we cross the widest gap which exists in the continuity of the plant kingdom. Intermediate forms between the liverworts and mosses on the one hand and the ferns and their allies on the other are missing, and although we may suggest various connecting links and reconstruct plausible evolutionary series, the transitional plants themselves have long since perished and we shall probably never know just how our present typical land vegetation had its origin.

The Advance from Bryophytes to Pteridophytes.—In the advance from bryophytes to pteridophytes the relative importance of the two generations has been completely reversed. The sporophyte is no longer an appendage of the gametophyte but is now the dominant and conspicuous generation, and has attained complete independence. The sexual plant is still independent, too, but it is relatively small and insignificant, and from this point onward throughout the vegetable kingdom it suffers a steady and progressive reduction. This shift in evolutionary advance from the gametophyte to the sporophyte marks the completion of that great forward step in the plant kingdom whereby a true land vegetation was evolved. The gametophyte is primarily an aquatic or at least a moisture-loving structure. Even in its highest development among the mosses, where it successfully invades the dry land, it has never been able to produce there a strong and vigorous vegetation. The sporophyte, however, seems early to have solved the problem presented by this radical change in environment, and when we meet it in the pteridophytes it has already developed a stout, branching, subterranean axis, the *root*, clothed with an abundance of root-hairs for absorption; large *leaves* presenting to the sun a relatively thick layer of chlorophyll-bearing tissue, which is well provided with air spaces and is protected by an epidermis in which are typical stomata; and a stout *stem* on which the leaves are lifted

high in air and which has made possible the development of the tall and vigorous plant body with which we are familiar. This advance in external complexity is paralleled by an equally notable internal one, for instead of the relatively simple structure of the moss plant, we find the highly differentiated internal anatomy described in earlier chapters. This is chiefly distinguished by the development of those tissues for support and conduction which we call *fibro-vascular*, and which include the wood and the bast. So distinctive of pteridophytes and seed plants is this type of internal structure that these groups are sometimes known collectively as the *vascular* plants, in distinction from the non-vascular thallophytes and bryophytes.

The remarkable advance in vegetative structures which the pteridophytes display is not paralleled in their methods of reproduction. The gametophytes form archegonia and antheridia, though somewhat smaller and simpler ones than those of the mosses, and motile sperms swim to the archegonia and there effect fertilization. The amount of sterile tissue in the sporophyte has, of course, enormously increased, but typical spores are still produced in definite sporangia and scattered abroad just as they are among the mosses. In the higher members of the division, two kinds of spores appear: *Microspores*, which give rise to antheridium-producing or male gametophytes, and *megaspores*, which give rise to archegonium-producing or female gametophytes. This condition of *heterospory* foreshadows the evolution of the seed, which distinguishes the last and highest plant group, the seed plants.

Pteridophytes are not very numerous in species nor do they form a very conspicuous part of the earth's vegetation today except in certain moist and warm regions. A study of fossil plants, however, shows us that members of this division were much more common in past ages, and indeed at certain periods were the most notable element in the plant population. Moreover, at that time they included many stout, woody, tree-like species which formed great forests. In competition with seed plants, the group soon fell from its dominant position and the few descendants which it has left to the present day are for the most part reduced and degenerate.

Three classes are recognized among the existing pteridophytes; the *Filicineae* or Ferns, the *Lycopodineae* or Club Mosses and the *Equisetineae* or Horsetails. These are so different from one

another that they are sometimes regarded as three distinct divisions, but their many points of resemblance make it perhaps more satisfactory to group them together.

Filicineae or Ferns.—This class, the largest of the three, includes the most conspicuous and familiar of the pteridophytes. The leaves, here known as *fronds*, are typically large and are

FIG. 198.—A fern plant, the polypody (*Polypodium vulgare*). This is the sporophyte generation. The stem is a creeping rootstock. On the backs of the leaves are born sori, or clusters of sporangia.

often deeply cut and dissected. The spores are all alike, except in the small group of water-ferns where heterospory exists. With a few exceptions, the gametophyte grows on the surface of the soil and is provided with chlorophyll, thus existing as an entirely independent plant. Three orders are recognized, the *Filicales*, *Ophioglossales*, and *Hydropteridales*.

1. *Filicales or True Ferns* (Figs. 198 and 199).—Almost all of the ferns belong here, the other two orders being very small ones. In our common species the stem is much reduced and is

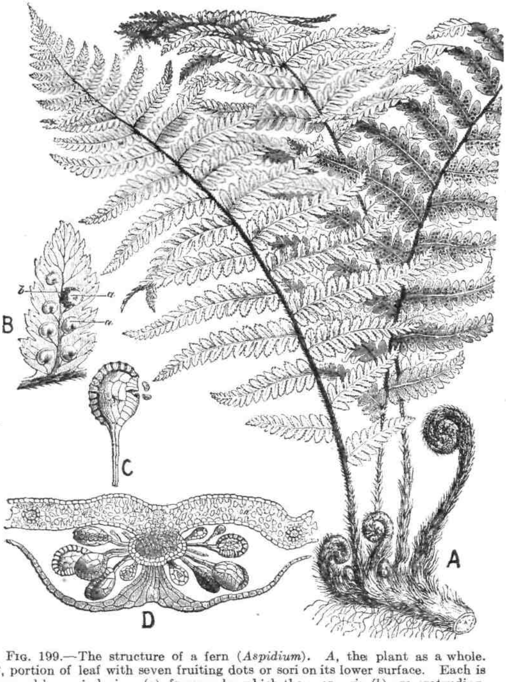


FIG. 199.—The structure of a fern (*Aspidium*). *A*, the plant as a whole. *B*, portion of leaf with seven fruiting dots or sori on its lower surface. Each is covered by an indusium (*a*), from under which the sporangia (*b*) are protruding, in one case. *C*, a single sporangium. *D*, transverse section through a sorus, showing section of leaf-blade above and of indusium below, with cluster of sporangia attached between them. (*From Strasburger, after Wossidlo*).

prostrate or subterranean, so that the leaves appear to rise directly from the ground. In many tropical species, however, an erect trunk is produced which bears a crown of large leaves at its

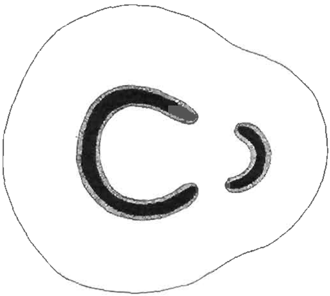


FIG. 200.—*Transverse section (diagrammatic) of the stem of a fern (Adiantum).* The fibrovascular system is here arranged in a hollow tube, the wood surrounded by bast both within and without. At the right, a segment of the cylinder is passing off to a leaf as a *leaf-trace*, causing a temporary break, or *leaf-gap*, in the cylinder. Wood black, bast dotted.

summit. The fern stem lacks a cambium, and the secondary wood and bast so common in the seed plants are consequently absent. The *fibro-vascular system* may occasionally be a solid

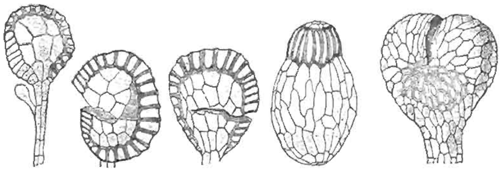


FIG. 201.—Fern sporangia of various types. The ring of heavy-walled cells is the *annulus*, by the contraction of which the wall of the sporangium is ruptured at maturity and its spores scattered. (*From Strasburger*).

axis, but is commonly a ring or tube surrounding a central pith (Fig. 200) and is often broken up by gaps into a series of separate bundles. The bast here occurs not only on the outside of the

wood but also inside, next the pith, and thus completely surrounds the wood. The cells of both wood and bast are somewhat less

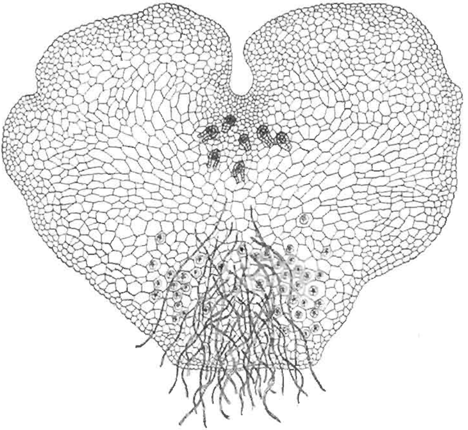


FIG. 202.—The gametophyte of a fern. View of the under surface, which lies next the surface of the ground. Here are borne the archegonia (near the notch) and the antheridia (farther back, among the rhizoids).

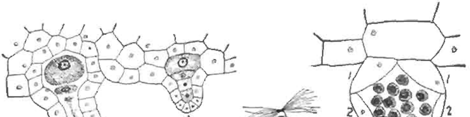


FIG. 203.—Sexual organs of a fern. *A*, section of archegonium just before maturity. Within can be distinguished the large egg cell, below which are the ventral canal cell and two neck-canal cells. In *B*, the archegonium is mature and its neck has opened. The egg and ventral canal cells are evident, but the neck-canal cells have broken down. *C*, section of antheridium, showing basal cell (1), ring cell (2), and cap cell (3). *D*, one of the sperms, more highly enlarged.

highly specialized than in the seed plants. Particularly in the stouter-stemmed species, the fibro-vascular system sometimes

becomes very complex and develops several concentric rings of bundles, the members of which are connected with one another in an intricate fashion. Masses of heavy-walled *sclerenchyma* cells are often formed in pith and cortex and aid in maintaining the rigidity of the stem.

The sporangia (Fig. 201) are borne on the back or dorsal surface of the leaf in definite clusters (Fig. 199) known as *fruiting-dots*

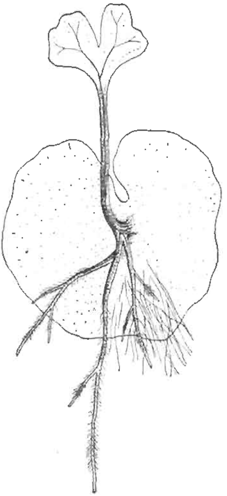


FIG. 204.—Young sporophyte of a fern, which has developed from a fertilized egg, growing out of its parent gametophyte.

or *sori* (singular, *sorus*). Each sorus is usually covered until maturity by a fold of thin, skin-like tissue, the *indusium* (Fig. 199), which arises from the leaf surface. The individual sporangium is very small in comparison with those of bryophytes and produces only a few spores. In most cases it displays around its wall a characteristic ring of cells, the *annulus* (Fig. 201), which is so constructed that upon drying it contracts like a spring, finally

rupturing the sporangium wall and forcibly ejecting the spores. The shape and position of the sorus and indusium, as well as the type of annulus, vary greatly among the different groups of ferns and serve as useful characters by which to distinguish genera and families.

The spores germinate into a thin, small, thallus-like gametophyte or *prothallus* (Fig. 202) which possesses chlorophyll and is

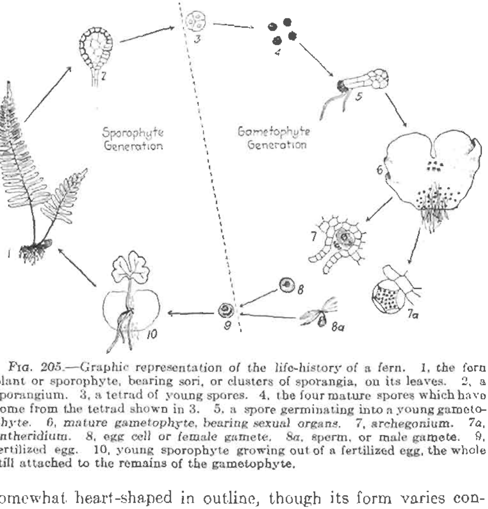


FIG. 205.—Graphic representation of the life-history of a fern. 1, the fern plant or sporophyte, bearing sori, or clusters of sporangia, on its leaves. 2, a sporangium. 3, a tetrad of young spores. 4, the four mature spores which have come from the tetrad shown in 3. 5, a spore germinating into a young gametophyte. 6, mature gametophyte, bearing sexual organs. 7, archegonium. 7a, antheridium. 8, egg cell or female gamete. 8a, sperm, or male gamete. 9, fertilized egg. 10, young sporophyte growing out of a fertilized egg, the whole still attached to the remains of the gametophyte.

somewhat heart-shaped in outline, though its form varies considerably. It is rarely more than a few millimeters in diameter and lies flat upon the surface of the soil, to which it is attached by delicate rhizoids growing from the under surface. Plentiful moisture and a partially shaded situation are necessary for the successful growth of a fern prothallus. The sexual organs (Fig. 203) are produced on the under surface, the archegonia near the "notch" and the antheridia farther back, among the rhizoids. The archegonia are much smaller than those of bryophytes and only their necks project above the surrounding tissue. They

appear when the prothallus is fully grown and considerably after the antheridia have liberated their sperms. At maturity, the neck of the archegonium opens and the neck-canal cells break down, producing a substance attractive to the sperms. The antheridium is also very much smaller and simpler than it is among bryophytes. Its wall consists of but three cells—a cover-cell, a circular cell which forms the main wall, and a funnel-shaped basal cell. The contents of the antheridium divides into a large number of sperms, each possessing a tuft of cilia by which it can swim about in a thin film of water (Fig. 203). A sperm enters an archegonium and there effects fertilization, after which the fertilized egg, by repeated cell divisions, forms a mass of tissue which gradually becomes differentiated into the body of the young sporophyte. This soon develops a vigorous root and shoot (Fig. 204) and grows into the mature fern plant. The life-cycle of a fern is graphically represented in Fig. 205.

The order includes nearly 3,000 species and its members are widely distributed over the globe, being particularly rich in species and individuals throughout all tropical regions. It is by far the largest group of pteridophytes and since early times has occupied an important place in the earth's vegetation.

2. *Ophioglossales or Adder's Tongues.*—Here are placed a small group of fern-like plants which are of interest to botanists from their possession of certain characteristics markedly different from those of other ferns. A single leaf, simple in the adder's tongue fern but typically fern-like in the rest of the order, is produced each season by the subterranean stem. From the petiole of this leaf arises a spore-bearing stalk crowned with a cluster of heavy-walled sporangia, very different in type from the thin-walled structures of true ferns. The gametophyte is thick and tuberous, and is partly subterranean. The Ophioglossales are often placed by themselves in a separate class.

3. *Hydropteridales or Water Ferns.*—This is another small group, chiefly important for its specialized method of reproduction. Its sporophyte is aquatic and bears little or no resemblance to that of the true ferns. *Marsilia* (Fig. 206), the clover-leaf fern, is the commonest representative. From the petiole of its curious four-lobed leaf arise one or more bean-like *sporocarps* containing sporangia of two sorts; the *megasporangia*, each producing a single large *megaspore*, and the *microsporangia*, each producing a group of smaller *microspores*. These are dispersed in

the water and there germinate. The megaspore produces a small female gametophyte still contained largely within the thick spore wall, and at the point where the wall bursts a single archegonium appears. The microspore gives rise to a single antheridium, which liberates into the water a group of sperms. The young sporophyte which develops from the fertilized egg is nourished

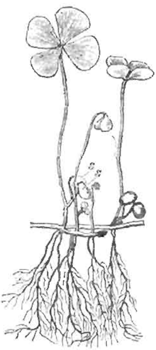


FIG. 206.

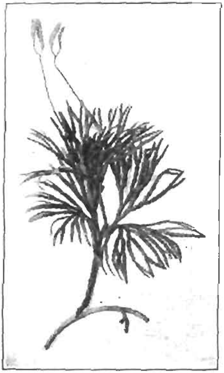


FIG. 207.

FIG. 206.—*Marsilia.* The spore-fruits or sporocarps (*s*) growing out from the petiole of the leaf contain microsporangia and megasporangia. (*From Strasburger, after Bischoff*).

FIG. 207.—A club-moss (*Lycopodium*). The underground stem has sent up a much-branched shoot on which are the small, scale-like leaves. Upon this are borne two groups of cones.

for a time on the abundant supply of food stored in the female gametophyte, but soon becomes independent through the establishment of a root and leaf of its own. This *heterosporous* type of reproduction is the highest found among the Filicineae.

Lycopodineae or Club Mosses.—This group is by no means as rich in species as the ferns. The *sporophyte* (Fig. 207) has a well developed stem, typically prostrate or subterranean but sending up numerous erect branches which sometimes reach a decimeter or more in height. In contrast to the ferns, the leaves are very small, numerous, and crowded closely on the stems, presenting a

moss-like appearance which has given the common name to the group. The internal structure of the stem in *Lycopodium* is unique, for its fibro-vascular system is a solid, pithless core, made up of alternating bands of wood and bast extending across the central cylinder (Fig. 208). The anatomy of the other genera is much simpler.

Sporangia are few and large as compared with those of the ferns, and are borne on the upper or ventral leaf-surface. In

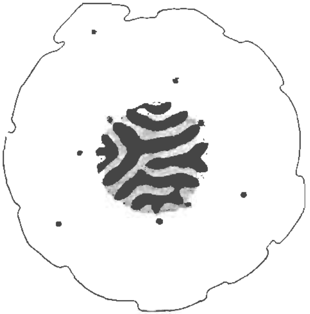


FIG. 208.—Transverse section (diagrammatic) of the stem of *Lycopodium*. The fibro-vascular cylinder consists of alternating bands of wood and bast. From this cylinder a small leaf-trace departs to each leaf. Wood black, bast dotted.

the simpler species, a sporangium may arise on an ordinary vegetative leaf but in most cases these spore-bearing leaves (which here, as elsewhere among the higher plants are known as *sporophylls*) become stout and scale-like, and are grouped in a cone or *strobilus* at the tip of a branch. The two main orders *Lycopodiales* and *Selaginellales* are distinguished chiefly by their methods of reproduction.

1. *Lycopodiales* (Fig. 209).—These are *homosporous* plants, the spores which they produce being all of one sort, as in the Filicales. The gametophytes vary considerably but tend to develop a stout tuberous, subterranean portion, which may be surmounted by a green aerial region on which the sexual organs are borne (Fig. 210). These are larger and better developed than

among the ferns, and the sperms resemble those of bryophytes in being biciliate. After fertilization the young sporophyte is carried rather deeply into the prothallial tissue by a long cell, the *suspensor*, and develops through its early stages largely at the expense of the gametophyte. To this order belongs the large genus *Lycopodium*, the familiar club moss or ground pine.

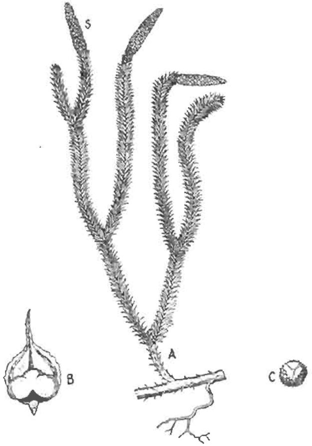


FIG. 209.—*Lycopodium*. *A*, part of a plant of *Lycopodium annotinum* showing prostrate stem and leafy, erect shoots bearing cones or strobili (*s*). *B*, sporophyll or cone-scale, bearing a sporangium on its upper surface. *C*, one of the very numerous spores produced in this sporangium, greatly enlarged.

2. *Selaginellales* (Fig. 211).—This order is represented by the genus *Selaginella*, which resembles *Lycopodium* rather closely in vegetative structures but differs from that genus in being heterosporous. Certain of the sporangia (the megasporangia, Fig. 211, B) produce four large megaspores each, and the others (the microsporangia, Fig. 211, C) produce an abundance of much smaller microspores. The history of the gametophytes is in many ways like that described for the water ferns. The megaspore produces a small mass of cells, most of which are still

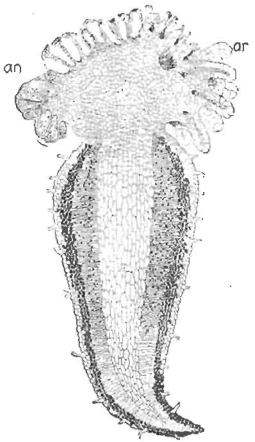


FIG. 210.—Gametophyte of *Lycopodium*, showing the stout, subterranean, tuber-like portion and the upper region in which antheridia (*an*) and archegonia (*ar*) are produced. (*From Strasburger, after Bruchmann*).

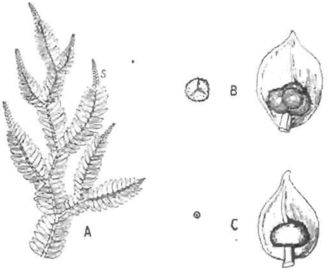


FIG. 211.—*Selaginella*. *A*, leafy branch bearing strobili (*s*). *B*, megasporophyll or cone-scale bearing a megasporangium. One of the four megaspores produced in this sporangium is shown at the left. *C*, microsporophyll or cone-scale bearing a microsporangium. One of the many microspores produced in this sporangium is shown at the left.

retained within the remains of the stout megaspore wall (Fig. 212). On the exposed tissue, a group of archegonia appear. Each microspore forms a single antheridium in which a group of biciliate sperms develops. The young sporophyte is thrust deeply into the tissues of the gametophyte until it has begun its differentiation. Such a life history as this is clearly a step in the direction of seed production.

The genus *Isoetes*, the Quillwort (Fig. 213), is usually included among the lycopods although its remarkable characteristics have

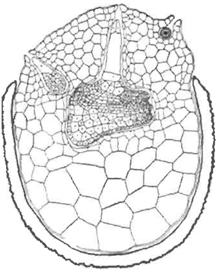


FIG. 212.—Female gametophyte of *Selaginella*. The stout wall of the microspore still encloses part of the gametophyte. At the right is an archegonium; at the center and left, young embryos which have arisen from fertilized eggs in other archegonia. The embryo is carried down into the tissue of the gametophyte by an elongated cell, the *suspensor*. In the larger embryo, the shoot (at right) and root (at left) are beginning to become differentiated, as well as the large, absorbing *foot*, at the lower left. (*Mainly after Pfeffer*).

caused some botanists to place it in a distinct order. The plants grow in water or very moist places and each consists of a tuft of long, quill-like leaves, arising from a short and flattened stem. In the hollow bases of these leaves the sporangia are borne. *Isoetes* is heterosporous, its gametophytes being similar in general structure to those of *Selaginella* except that the sperms have many cilia.

The lycopods were particularly prominent in the forests of the Coal Period, the great tree-like lepidodendrids and sigillarians belonging to this order. It is noteworthy that these ancient members of the group possessed a cambium and well developed secondary wood, tissues which are quite absent in living lycopods.

Equisetineae or Horsetails.—This very distinct class consists of but one order, the *Equisetales*, and this of but the single genus *Equisetum*, the horsetails or scouring rushes (Fig. 214). Some of its species grow in dry sterile soil and others in marshy situations. From a perennial rootstock arise the very characteristic stems, which are jointed, ridged, and hollow. Leaves are repre-

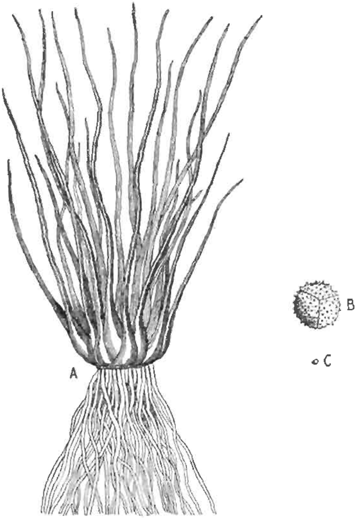


FIG. 213.—*Isoetes.* *A*, general appearance of the plant. *B*, a megaspore. *C*, a microspore.

sented merely by a circle of scales which surround the stem at each joint or node, the green stems carrying on most of the process of photosynthesis. Aside from the large central air space, a smaller one occurs just inside each furrow in the stem (Fig. 215). Opposite each ridge is a small and very poorly developed fibrovascular bundle, the stoutness and strength of the stem being due chiefly to the layers of heavy-walled sclerenchyma which it

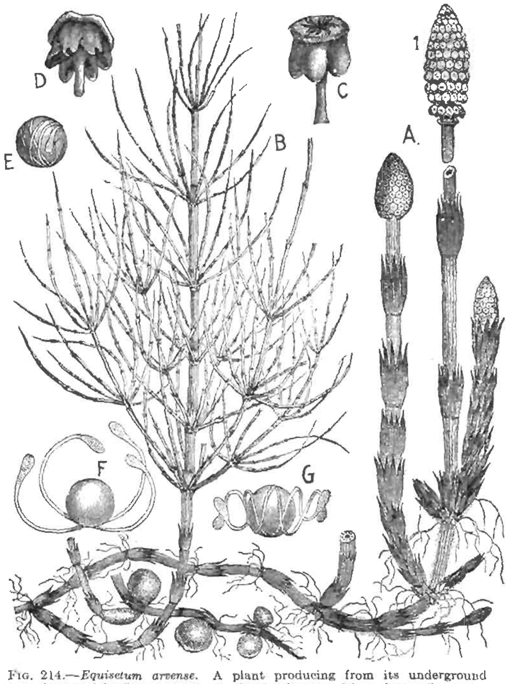


FIG. 214.—*Equisetum arvense.* A plant producing from its underground rootstock several fertile stems (*A*), terminating in cones (1); and a sterile, much-branched shoot *B*. *C*, one of the sporophylls from the cone, bearing a group of sporangia. *D*, the same, with the sporangia ruptured and their spores shed. *E*, *F*, and *G*, spores, greatly enlarged, with the elaters in various positions. (*From Strasburger, after Wossidlo*).

contains. Across the stem at each node extends a solid partition or diaphragm. The stems may be branched or unbranched.

As in the lycopods, the sporangia are borne in terminal cones (Fig. 214). The sporophylls, however, are not at all leaf-like but

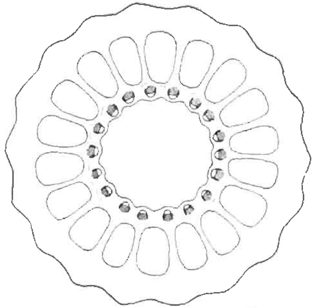


FIG. 215.—Transverse section (diagrammatic) of the stem of *Equisetum*. Note the large central cavity, the air chambers opposite the stem furrows, and the smaller ones in the bundles. The fibro-vascular system is much reduced, consisting of a ring of small bundles, each with two minute arms of wood and a patch of bast between. Wood black, bast dotted.

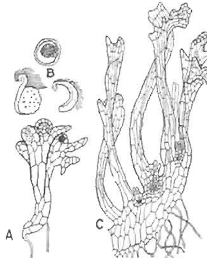


FIG. 216.—Gametophytes of *Equisetum*. *A*, male gametophyte, showing antheridia. *B*, sperms. *C*, female gametophyte, showing the long, branching lobes with archegonia at their bases. (*A and C after Hofmeister, B after Schacht*).

are somewhat shield-shaped and project outward at right angles to the cone axis. On their under or inner surfaces are borne a row of sporangia. The spores are all alike externally, but a

given spore will generally produce either a strictly male or a strictly female gametophyte. Attached to each spore are four thread-like structures, the *elaters* (Fig. 214), which coil tightly around it when moist but expand when dry, and thus aid in spore dispersal.

The gametophyte (Fig. 216) is an irregular thallus which develops chlorophyll, shows no tendency toward the subterranean habit of the lycopod prothallus, and is provided with long, branching lobes. The two sexes are usually on separate plants and the gametophytes are therefore said to be *dioecious*. The sexual organs resemble in general those of other pteridophytes. The antheridia occur at the tips of the lobes and the archegonia at their bases. Each sperm has a tuft of cilia. In embryonic development no suspensor is formed, and the whole process considerably resembles that found among the ferns.

The Equisetineae, like the Lycopodineae, were represented in earlier periods of the earth's history by large, tree-like species with well developed cambium and secondary wood. Many of these were also heterosporous.

QUESTIONS FOR THOUGHT AND DISCUSSION

769. Which of the three groups of pteridophytes is the most ancient, in your opinion? Why?

770. What other groups of plants already described (aside from the pteridophytes) were once probably very abundant but are now represented by only a comparatively small number of species?

771. Why is asexual reproduction so common among the pteridophytes?

772. Do you think that heterospory has arisen more than once in the evolution of the plant kingdom? Explain.

773. Which do you think is more primitive among pteridophytes, thin-walled sporangia or thick-walled ones? Why?

774. Can you suggest a reason for the fact that ferns are now so much more abundant than club mosses or horsetails?

775. Why are there no tree-ferns in temperate climates?

776. How does the trunk of a tree-fern differ from that of an ordinary tree?

777. Why does not the trunk of a tree-fern make good lumber?

778. Are common ferns annuals or perennials? Why?

779. Of what advantage to the fern plant is the indusium?

780. Of what advantage is it to the fern plant to have the archegonia and the antheridia on the same gametophyte mature at different times?

781. In what particulars do the Ophioglossales resemble the ferns? In what do they resemble the club mosses?

782. Do you think that a cone is more primitive than a group of leaf-like sporophylls or not? Why?

783. Of what advantage to the plant is it to have its sporophylls grouped into a cone rather than scattered along the stem?

784. How do a typical fern and a typical horsetail differ in the environment to which they are best adapted?

785. What are the advantages of a subterranean, saprophytic gametophyte over the free-living one characteristic of most ferns? Which form do you think is the more primitive? Why?

786. In what particulars does *Isoetes* resemble the ferns? In what does it resemble the club mosses?

787. In what particulars do the Equisetales resemble the Filicales? In what do they resemble the Lycopodiales?

788. Of what significance is the fact that the gametophytes of *Equisetum* are usually dioecious?

789. How do the elaters in the sporangium of *Equisetum* aid in spore dispersal?

REFERENCE PROBLEMS

133. Of what economic importance are the pteridophytes?

134. Construct for *Lycopodium* a graphic life-cycle similar to that given in the text for a fern (Fig. 205).

135. Construct a similar graphic life-cycle for *Selaginella*.

136. Construct a similar graphic life-cycle for *Equisetum*.

137. Give the derivations of the following terms and explain in what way each is appropriate:

Heterosporous	Indusium	Prothallus
Sorus	Annulus	Sporophyll
	Strobilus	

CHAPTER XVII

THE SPERMATOPHYTA

This enormous group, to which the early portions of our text were largely devoted, includes the most familiar and abundant part of the earth's plant population. Directly or indirectly, the seed plants furnish almost all the food supply of the human race, all of its timber and fiber plants, and a great majority of the animal and vegetable products which form the basis of our civilization. It is this division of the plant kingdom which is present most intimately in the thoughts and lives of men, and which for a long time provided practically the entire subject-matter for the science of botany.

In vegetative characters the spermatophytes are not remarkably different from the pteridophytes. They display the same vigorous development of root, stem, and leaf, and although they commonly show a greater specialization and differentiation of their tissues, particularly in the higher groups, the fundamental plan established in the ferns, with its emphasis on a well developed fibro-vascular system, is retained and further developed. Growth of the stem in diameter by means of an active cambium occurs in most seed plants, although it is much reduced or absent in the more delicate herbaceous species.

The Origin of the Seed.—The distinguishing feature of the spermatophytes, as their name indicates, is the development among them of a new reproductive structure, the *seed.* In an earlier chapter we have outlined briefly the evolution of the seed-habit and its significance; but in view of the greater familiarity with the lower plants which we now possess, it will perhaps be worth while to describe the seed and its origin somewhat more fully before we take up in detail the various plant groups in which this structure occurs.

Relation to Structures in the Lower Groups.—The seed-producing habit is a direct development from such a condition of heterospory as has been attained by the higher pteridophytes. It will be remembered that in the water ferns, in *Selaginella,* and in *Isoetes,*

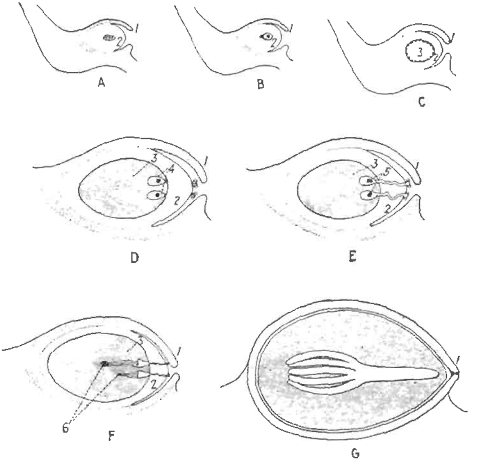


FIG. 217.—Development of the female gametophyte and seed in a gymnosperm (Pine). Longitudinal sections through the base of the cone-scale. *A*, young ovule, consisting of an integument (1) and a megasporangium or nucellus (2), within which is a row of four megaspores which have developed from a megaspore mother-cell. *B*, three of the megaspores have aborted, the fourth is enlarging. *C*, the megaspore has germinated into a young gametophyte or embryo-sac (3), which now consists of a layer of free nuclei surrounding a large vacuole. *D*, the young sac has developed into the mature female gametophyte (3), the bulk of which consists of endosperm. At one end are two archegonia (4) within each of which is an egg-cell. Pollen grains have entered the micropyle and alighted on the tip of the nucellus. *E*, *fertilization*. Two pollen grains have germinated, sent their tubes down through the nucellus, and discharged their contents into the two archegonia, in each of which one of the male nuclei is fusing with the egg nucleus (5). *F*, from the fertilized egg have grown two young embryos (6), one larger than the other, which have been pushed down into the middle of the endosperm. *G*, mature seed. The integument of the ovule has developed into the seed coat, the micropyle has closed, the endosperm has become greatly enlarged, the nucellus has almost disappeared and the embryo has grown to its full size. The smaller embryo in *F* failed to develop. This seed will now detach itself for them cone-scale and under favorable conditions will produce a new plant.

the spores are not uniform but that microspores and megaspores, borne in separate sporangia and on separate sporophylls, germinate into male and female gametophytes, respectively. The seed plants are likewise heterosporous. As in the lower groups, they develop microspores (now called *pollen grains*). These are borne in a microsporangium (now called an *anther*), arising from a microsporophyll (now called a *stamen*). No very radical change is evident here, but in the case of the female structures we find some marked innovations.

The Ovule and Its Contents (Figs. 217 and 229).—The megasporangium, now known as the *nucellus*, produces only one functioning megaspore, for the other three members of the tetrad which begin to develop soon disappear. Furthermore, the sporangium does not burst and liberate this spore but retains it, instead, and allows it to germinate and produce the female gametophyte within the tissues of the sporangium (nucellus), nourished by the parent sporophyte. The female gametophyte (now called the *embryo-sac*) is a small, roundish group of cells filled with food and bearing at one end one or more archegonia or structures comparable to them. The whole is embedded in the tissue of the nucellus and is never freely exposed. Among the highest forms it suffers such reduction that resemblance to a gametophyte becomes very faint. The nucellus and its enclosed embryo-sac are completely surrounded and protected by one or two coats or *integuments* except for a small opening, the *micropyle*, which occurs just opposite the point where the archegonia are borne in the embryo-sac beneath. The whole structure—integument, nucellus, and embryo-sac—is known as the *ovule*, and after fertilization, for which it is now prepared, the ovule will develop into a seed. It is closely attached to the megasporophyll, which is now called a *carpel*.

Pollen (Fig. 218).—The microspore or pollen grain, produced in the microsporangium, in the mean time germinates and produces within itself the male gametophyte. This is greatly reduced and consists at most of a very few cells, in the higher forms of only two—the generative cell and the tube-nucleus. These are all that remains of the male sexual generation. Germination of the microspore usually takes place, at least in part, before it is liberated by the breaking open of the anther wall. After this event, the pollen grain is transferred, by wind, insects or other means, either directly to the ovule or to a receptive

structure (the *stigma*) which is nearby. Since the egg cells are buried in the nucellar tissue, it is evident that the male gametes cannot approach them directly, as in the lower plants, and a new structure has accordingly been developed which conveys them to the egg. This is the *pollen-tube.* It arises from the pollen-grain as a slender, thin-walled projection and into it the contents of the grain passes, led by the tube-nucleus.

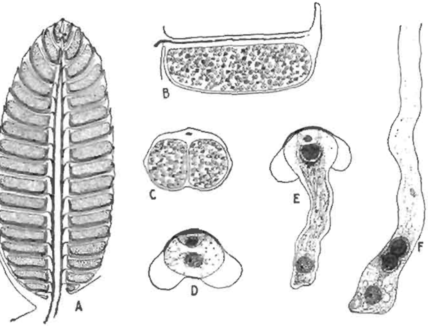


Fig. 218.—Development of the male gametophyte in a gymnosperm (Pine). *A*, longitudinal section (diagrammatic) of a staminate or "male" cone. *B*, one of the sporophylls from *A*, much enlarged. The sporangium is filled with microspores or pollen, in various stages of development. *C*, section across the sporophyll at right angles to that in *B*, showing the two sporangia which are borne on each sporophyll. *D*, a mature pollen grain. The outer wall (in the case of pine pollen) is puffed out somewhat at two points, forming balloon-like "wings" which add to the buoyancy of the grain. The single nucleus of the megaspore has now divided to form the generative cell, lying next the wall, and the tube nucleus, in the center of the cell. *E*, a germinating pollen grain. The tube nucleus follows close behind the end of the growing tube. The generative cell has divided into a stalk cell (lighter) and a body cell (darker). *F*, the end of the pollen-tube just before fertilization. The body cell has developed into the two male cells or gametes, which have now come down the tube and are ready to effect fertilization.

Fertilization and Seed-production (Figs. 217 and 229).—The pollen tube grows rapidly and penetrates the tissues, much as a fungus filament penetrates the tissues of its host, until it reaches the embryo-sac and the egg-cells. A large nucleus in the tube, often the only one at this point except the tube nucleus, now divides into two male gametes, and as the end of the tube bursts

into the sac one of these unites with an egg. The fertilized egg now divides and grows into a young sporophyte, the *embryo*, possessing a primitive root, stem, and leaves. The embryo soon stops its growth and becomes dormant, embedded in the tissues of the sac which are by now filled with reserve food or *endosperm*. The integument in the mean time has developed into the tough *seed coat* and the whole structure soon separates from the mother plant as a mature seed. Under favorable conditions of temperature and moisture this seed will germinate, the embryo breaking out through the seed coats and establishing itself in the soil as a new plant which grows for a time at the expense of the stored food but soon becomes independent.

The Advances from Pteridophytes to Seed Plants.—The essential advances made by seed plants over the higher pteridophytes are therefore: (1) The retention of the megaspore within the megasporangium and its germination there into the female gametophyte; (2) the enclosure of the sporangium and sac by a new structure, the integument; (3) the transference of the reduced male gametophyte directly to the vicinity of the female gametophyte, to which the male gametes obtain access by another new structure, the pollen-tube; (4) the development of the young sporophyte in contact with, and at the expense of, the parent sporophyte, and (5) its final release, dormant, well supplied with food, and protected by a heavy coat. It is noteworthy that the reversal of the reproductive situation as we find it in the bryophytes is now complete, for instead of the sporophyte being attached to the gametophyte, the gametophyte (and even the succeeding sporophyte) is here attached to the parent sporophyte. Indeed, in the most advanced types both gametophytes are so much reduced that little beside the sexual cells remains, and the alternation of generations has practically disappeared.

The Flower.—The sporophylls of seed plants tend to be arranged in distinct clusters on short branches. In the lower members of the group these clusters are entirely similar to the cones of some of the pteridophytes, but higher up a very specialized shoot, commonly called the *flower*, has been evolved. In its fully developed form this contains not only the stamens and carpels, but modified leaf-like structures for protection of the sexual organs and for attraction of insects. From the possession of this structure the spermatophytes are sometimes called the "flowering plants."

To describe adequately the various orders of which this huge division is composed is quite impossible within the limits of our text. Aside from its numerous and varied living members it also includes a great number of fossil types, many of which are important in reconstructing for us the steps in the evolutionary history of the seed plants. We shall attempt to present the salient characters of the more important groups only, and to indicate their probable relationship to each other and their place in the phylogeny of the whole series.

Gymnospermae or Gymnosperms.—Two classes of seed-plants are commonly recognized, the gymnosperms and the angiosperms, differing chiefly as to the manner in which the ovules are borne. The gymnosperms are the most ancient of seed plants, and a varied and heterogeneous group. All agree in possessing ovules and seeds which are borne openly on the megasporophyll or carpel, freely exposed to the air and to the direct contact of pollen grains, and not inclosed in an ovary as they are among the angiosperms. There is good reason to believe that the earliest gymnosperms arose from fern-like ancestors, for several remarkable fossil plants from the Coal Period have been discovered which possessed typically fern-like foliage, and were long thought to be true ferns, but which are now known to have borne undoubted, though primitive, seeds. This group, sometimes called the *Cycadofilicales* or cycad-ferns, has long been extinct, nor have any of its near relatives survived. The most primitive living gymnosperms are the Cycads.

1. *Cycadales or Cycads.*—Cycad stems are typically stout and unbranched, and bear at the top a crown of large, pinnate leaves (Fig. 219). A few species have tall, columnar trunks and thus superficially resemble tree ferns or palms. Internally, the stem possesses a large pith and cortex but its woody tissue is rather weakly developed, although the fibro-vascular system is often complicated by the occurrence of several concentric rings of bundles instead of a single ring.

The male and female sexual structures occur on separate plants, and the sporophylls are borne in terminal cones (Fig. 220). In the genus *Cycas*, the ovulate sporophylls ("female" cone scales) are large and lobed, showing a slight resemblance to foliage leaves, and bear ovules along their edges (Fig. 221). In the other members of the order the cones are more compact and the sporophylls or cone scales have lost their leaf-like character. Each

microsporophyll (Fig. 222) bears many sporangia or anthers and produces a large amount of pollen. The ovules are generally large and thick-walled, and the megaspore, arising as one of four potentially spore-producing cells in the middle of the nucellus, develops into a large embryo-sac. At the tip of the nucellus, just under the micropyle, a large, liquid-filled *pollen chamber* arises. The pollen grain enters this chamber through the micro-

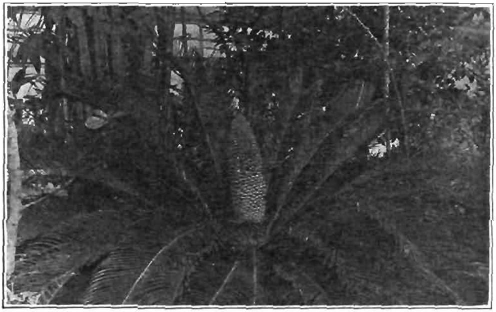


FIG. 219.—*Cycas revoluta*, one of the Cycadales. Male plant with cone. (*Photo by C. S. Torrey*).

pyle and there germinates. Its two male cells are each provided with a spiral band of cilia and swim about in the liquid, a remarkable persistence of the habit of swimming sperms which harks back through pteridophytes and bryophytes to their remote algal ancestry. A pollen-tube is formed and penetrates the adjacent nucellar tissue, but it seems rather to absorb food than to assist in the transference of the male cells, for the pollen-chamber gradually enlarges itself until it reaches the embryo-sac, where one of the sperms enters an archegonium and effects fertilization.

Cycads are confined to the warmer regions of the globe. They are an inconspicuous group today but in earlier ages, notably in the Mesozoic Era, were abundant and diversified. Their close relatives, the *Bennettitales* (now extinct), were for a time

among the most conspicuous of plants and produced some complex flower-like bisexual reproductive organs.

Closely related to the cycads is the Japanese maiden-hair tree, *Ginkgo*, usually placed in a separate order by itself. It

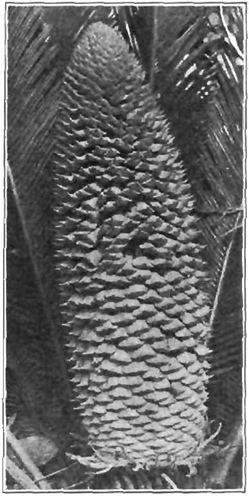


FIG. 220.—Staminate cone of *Cycas revoluta*. (*Photo by G. S. Torrey*).

resembles the cycads in the possession of a pollen-chamber and of motile sperms, but differs in its tree-like habit of growth and in the absence of typical cones.

2. *Coniferales or Conifers.*—These are familiar to us from their wide distribution in temperate zones and from the fact that they include many of our most important forest trees. The vegetative body differs radically from that of the cycads for it is usually a tree, with a straight trunk and spreading lateral branches which give a spire-like shape to the whole (Fig. 8). The leaves are typically small, evergreen scales or needles. The bulk of the

stout woody stem is secondary wood, laid down by an active cambium. Its water-conducting cells are all tracheids, those produced in the spring being comparatively wide and thin-walled

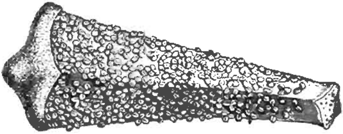


FIG. 221. FIG. 222.

FIG. 221.—*Cycas*. Sporophyll from ovulate cone, showing several ovules attached to its side. One of these has developed into a seed. (*From Strasburger, after Sachs*).

FIG. 222.—*Cycas*. Sporophyll from staminate cone, showing numerous pollen sacs or microsporangia. (*From Strasburger, after Richard*).

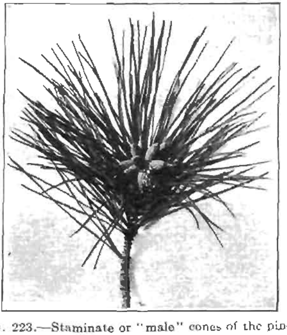


FIG. 223.—Staminate or "male" cones of the pine.

and those in the summer much narrower and thicker-walled (Fig. 63). The general structure of the vascular tissues approaches rather closely to that of the angiosperms.

As its name implies, the reproductive structures in this order are typically produced in cones. The microsporangial (staminate or "male") cones (Fig. 223) are short-lived and somewhat delicate structures, and each cone-scale (stamen or microsporophyll) bears two (rarely more) microsporangia on its lower or dorsal surface, in which the microspores or pollen grains are

FIG. 224.—Ovulate or "female" cones of the pine.

developed (Fig. 218). The pollen is in all cases transferred to the ovules by wind. Except for the rather small group Taxaceae, in which cone-scales or integuments become fleshy at maturity, the megasporangial (ovulate or "female") cones (Figs. 224 and 225) usually become hard and woody. Each cone-scale bears one or two ovules. In most cases the embryo-sac is distinctly smaller than that of the cycads and contains fewer cells (Fig. 217). The pollen alights on the nucellus and there germinates (Fig. 218). The generative cell at this time divides into two, a *stalk cell* and a *body cell,* which are believed to represent the remains of an antheridium. The body-cell in time follows the tube-nucleus down the pollen tube and divides into two male cells, one of which effects fertilization (Fig. 226). No pollen-chamber is formed, but the pollen-tube conveys the male cells, which are non-motile,

directly to the archegonia. After fertilization there are a few divisions of the egg within the archegonium itself, and the young *proembryo* thus formed is then carried deeply into the tissues of the embryo-sac by certain of its upper cells, which rapidly elongate. In this position it develops into the mature embryo of the seed.

FIG. 225.

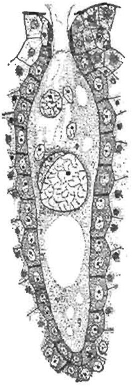


FIG. 226.

FIG. 225.—Longitudinal section (diagrammatic) of the ovulate or "female" cone of pine. Attached to the base of each scale is seen an ovule, its micropyle pointing inward.

FIG. 226.—Fertilization in a conifer. Archegonium into which a pollen-tube has just entered. One of the male nuclei may be seen uniting with the egg nucleus. The other, left behind in the cytoplasm, will die. (*From Sinnott*).

Like cycads, the conifers are an ancient group and are prominent in fossil floras since Mesozoic times. Although they include only about 350 species today, they cannot well be called degenerate for in many parts of the forested regions of both the north and the south temperate zones they contribute to the vegetation such notable trees as the pines, spruces, firs, larches, hemlocks, cedars, cypresses, and many others.

3. *Gnetales*.—Brief mention should be made of the most highly specialized order of gymnosperms, the *Gnetales*, which consist of three genera only; a tropical climber, a desert shrub, and an

anomalous desert plant. These are distinguished from other members of the class chiefly by the possession of vessels or ducts in the wood and by a marked reduction in the female gametophyte somewhat similar to that which occurs among angiosperms. It has been suggested that through forms related to the *Gnetales*, the angiosperms may perhaps have arisen from the gymnosperms.

Angiospermae or Angiosperms.—Angiosperms differ from gymnosperms chiefly in the fact that their seeds are not directly exposed to the air on the open surface of a scale but are enclosed in a definite case or vessel, the *ovary*.

With their 135,000 species, their highly perfected and typically insect-pollinated flowers, their enormously diversified plant bodies, their successful invasion of all habitats, and their assumption of practically every mode of life exhibited by plants, the angiosperms stand at the apex of the vegetable kingdom. They are a modern group and have arisen in comparatively recent geological time. Before the competition of this new, vigorous, and well-equipped phalanx, the older vascular plants have been swept aside, most of them to complete extinction, and the rest, with few exceptions, to comparative insignificance. It is only the thallophytes, with their specialization for aquatic, parasitic, and saprophytic habits of life, that can compare with angiosperms in number of species and individuals, and we must remember that were it not for these higher seed plants, practically all saprophytes and parasites would perish. The angiosperms are of primary importance as food producers for animals and man.

Since it is the members of this group which we have studied almost exclusively in the earlier chapters of the text, it will not be necessary to treat them here with as great detail as we have the other branches of the plant kingdom. It will be worth while, however, to bring together the essential features of the class as a whole, that we may readily compare it with the other seed plants and see it in its proper relation to the rest of the plant kingdom.

Vegetative Structures.—The vegetative body is much diversified. Seed plants not only include trees and smaller woody plants, (the only growth forms displayed by gymnosperms), but they have developed a new type, the *herb*, which is particularly well adapted to temperate or semi-arid regions, since it is small and soft-stemmed, produces flowers and fruit after a very short growing period, and can survive winter, dry seasons and other unfavorable periods either underground or in the form of resistant seeds.

In perennial herbs the underground parts survive and it is only the upper portions which die back; in biennial herbs, the plant lives through two seasons, storing up food the first and flowering the second, and in annual herbs the plant body lives through only one season, and survives unfavorable conditions in the seed. Herbs are now very rich in species and include the majority of our food plants and many others of economic importance.

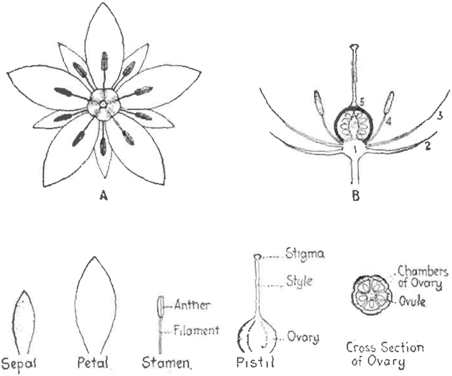


FIG. 227.—The structure of the flower of a dicotyledonous seed-plant (diagrammatic). *A*, face view of the flower, showing its calyx of five sepals, its corolla of five petals, its ten stamens and its pistil. *B*, longitudinal section, showing the relations between the parts. 1. Receptacle. 2, Calyx. 3, Corolla. 4, Stamen. 5, Pistil, with ovary cut lengthwise.

Internally, the vascular system reaches in angiosperms its highest degree of specialization. A cambium is well developed in the woody members but is much reduced among herbs. The wood consists not only of those general-utility elements, the tracheids, but also of thick-walled *fibers* whose function is to furnish rigidity to the stem; and of wide, thin-walled *ducts* or *vessels*, by which large quantities of water can be conveyed rapidly through the wood. In the bast, too, a new element, the *companion-cell*, intimately related to the sieve-tube, makes its appearance.

Reproduction.—The gymnosperms are all wind-pollinated, and many of the lower angiosperms resemble them in this respect and have inconspicuous, cone-like reproductive organs (Fig. 107) often not differing remarkably in general appearance and function from the gymnosperm type, except in the possession of ovaries.

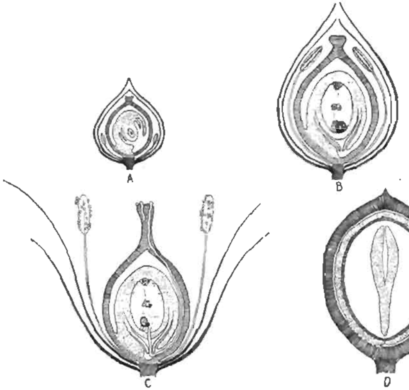


FIG. 228.—The process of seed-production in a flowering plant. Longitudinal diagrams of flower and fruit, the calyx and corolla solid black; the ovule, seed-coats and embryo dotted, and the ovary wall, style and stigma lined. *A*, young bud, the stamens and the single ovule beginning to develop. *B*, bud ready to unfold. The embryo-sac within the ovule is fully developed and the egg (below) and double endosperm nucleus (in center) are ready for fertilization. *C*, fully opened flower. The anthers have burst and pollination has taken place, pollen grains being transferred to the stigma. Two grains have germinated, and the pollen-tube from one of them has penetrated the style, entered the ovary, passed through the micropyle of the ovule and discharged its contents—the two male gametes—into the embryo-sac. Double fertilization is taking place, one male gamete uniting with the egg and the other with the endosperm nucleus. *D*, ripe fruit. Sepals, petals and stamens have dropped off; the ovary wall has hardened into the pericarp; the micropyle has closed; the integuments have become seed coats and the ovule has developed into the seed. The embryo, in the center of the seed, has grown from the fertilized egg, and the endosperm surrounding it (shown in white) from the endosperm nucleus.

The higher members, however, have come to depend upon insects to transport their pollen, and have evolved the characteristic *flower* (Fig. 227) which we have described in a previous chapter, with its protective calyx, composed of sepals; its attrac-

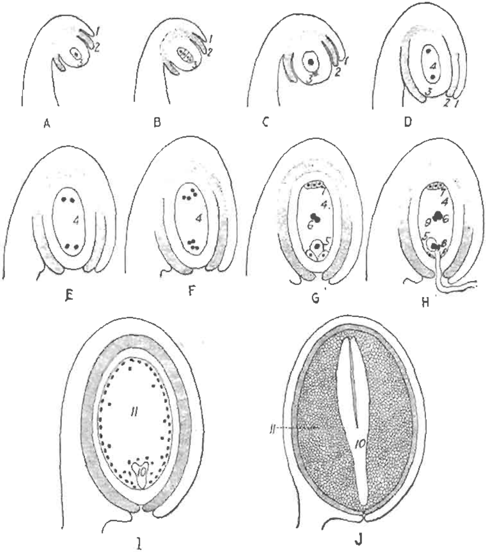


Fig. 229.—Development of the female gametophyte and seed in a dicotyledonous angiosperm. Longitudinal sections through the ovule and seed. *A*, very young ovule, the two integuments (1 and 2) beginning to appear and the megaspore mother-cell evident within the nucellus (3). *B*, the megaspore mother-cell has produced a row of four megaspores. *C*, three megaspores have aborted, the fourth is enlarging. *D*, the megaspore nucleus has divided into two, which now lie at opposite ends of the young embryo-sac (4). *E*, each nucleus has again divided into two. *F*, each of the four nuclei has again divided into two, so that there are now two groups of four nuclei, one at each end of the embryo-sac. *G*, one nucleus from each group has migrated to the center, and the two are uniting to form the endosperm nucleus (6). The three left at the end of the sac next the micropyle have formed the egg-cell (5) and the two synergid cells. The three at the opposite end have formed the antipodal cells (7). The embryo sac is now fully developed and the egg is ready for fertilization. *H*, a pollen tube has entered the micropyle and discharged two male cells into the embryo sac. One of these (8) is uniting with the egg and the other (9) with the endosperm nucleus. *I*, the fertilized egg has grown into a small embryo (10) and the fertilized endosperm nucleus into a sac lined with nuclei (11). *J*, the mature seed. The integuments have hardened into seed coats, the micropyle is closed, the nucellus has disappeared, the endosperm sac has become a mass of solid endosperm, packed with food, and the embryo has reached its full size.

tive corolla, composed of petals; its pollen-producing stamens, and its ovule-bearing pistil. The pistil may be a single carpel (which has grown about the ovules and enclosed them); a number of

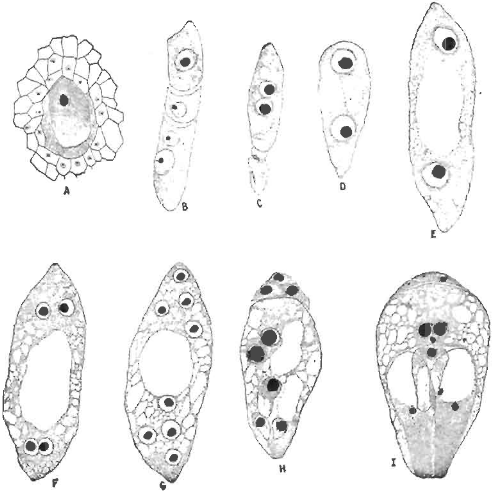


FIG. 230.—Development of the embryo sac, and fertilization, in the squash. *A*, megaspore mother-cell, which is situated in the middle of a very young ovule. *B*, the four spores which develop from the mother-cell. Three of these degenerate and disappear but the fourth, larger than the others, is the functional megaspore. *C*, the enlarged megaspore, in which the nucleus has now divided into two. *D*, a stage slightly later than *C*. The two nuclei have migrated to opposite ends of the young embryo-sac. *E*, a still later stage, with the embryo-sac much increased in size. *F*, each of the two nuclei has divided into two. *G*, each of these four nuclei has again divided into two, producing eight nuclei in all. *H*, the embryo-sac, nearly mature. At the upper end (away from the micropyle of the ovule) are three antipodal cells. At the lower end (toward the micropyle) are the egg nucleus and the two synergids. The two endosperm nuclei in the middle have not yet fused. *I*, fertilization. One small male nucleus is about to unite with the endosperm nucleus (still double) and the other is about to fertilize the the egg. (*From A. I. Weinstein*).

separate carpels; or a group of carpels which have become fused together. In any case, the pollen is necessarily prevented from

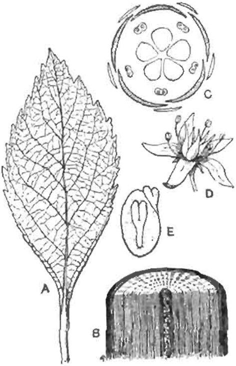
alighting directly upon the micropyle as it does in the gymnosperms, but instead is received upon a special projection of the pistil, the *stigma*. Here it germinates and sends down a pollen tube which ultimately reaches an ovule (Fig. 228).

The male gametophyte has practically disappeared, for the nucleus of the microspore now divides only into the tube nucleus and the generative cell, and the latter produces two non-motile male gametes. The female gametophyte is also greatly reduced (Figs. 229 and 230). The megaspore (the successful one of four originally produced in the nucellus) becomes much enlarged. Its nucleus divides into two, and one of these migrates to the end of the young embryo-sac next the micropyle of the ovule and the other to the basal or antipodal end. Here each nucleus undergoes two further divisions, so that at each end of the sac there are now four nuclei. One from each set then moves toward the middle and these two there fuse to form the *endosperm nucleus*. The three remaining at the micropylar end of the sac become definite cells, one of them the egg cell and the other two the *synergids*, probably the remains of an archegonium. The three antipodal cells represent all that remains of the abundant vegetative tissue of the sac as it is found in the gymnosperms. The gametophyte now consists of seven cells (or six cells and a naked nucleus) and is ready for fertilization. The two male cells pass down the pollen tube and enter the ovule. One fertilizes the egg nucleus, as usual, and from this union the embryo results. The other, however, instead of being eliminated, unites with the endosperm nucleus, and from the union of these two nuclei (one of which, it will be remembered, is already a product of fusion) develops the endosperm of the seed. The endosperm thus differs markedly in its history from that of gymnosperms. This phenomenon of *double fertilization* is a distinctive feature of reproduction in all angiosperms. The development of the embryo and the ripening of the seed go on much as among the lower seed plants.

The angiosperms are divided into two clearly marked subdivisions, the dicotyledons and the monocotyledons.

Dicotyledoneae or Dicotyledons.—As their name implies, these plants are characterized by the presence of two cotyledons in the embryo of the seed, as opposed to the single one of monocotyledons, and they also display several other distinctive features (Figs. 231 and 232). These are: (1) The presence of

netted venation in the leaf as opposed to the typically parallel-veined system of the monocotyledonous leaf; (2) the distribution of the vascular system in a ring or tube separating an internal pith from an external cortex, as opposed to the irregularly scattered system of separate bundles in the monocotyledonous stem; and (3) the development of the floral



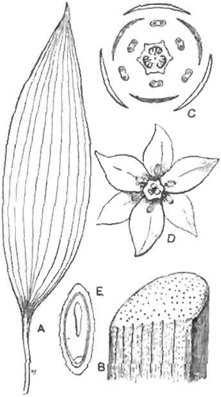


Fig. 231. Fig. 232.

Fig. 231.—Characteristics of a typical dicotyledonous plant. *A*, leaf, netted-veined. *B*, stem, showing ring of wood and bast. *C* and *D*, the flower, showing the floral parts in fives. *E*, section of seed, showing dicotyledonous embryo. (*From Gager's "Fundamentals of Botany", P. Blakiston's Son and Co., Philadelphia*).

Fig. 232.—Characteristics of a typical monocotyledonous plant. *A*, leaf, parallel-veined. *B*, stem, showing fibro-vascular bundles irregularly scattered. *C* and *D*, the flower, showing the floral parts in multiples of three. *E*, section of seed, showing monocotyledonous embryo. (*From Gager's "Fundamentals of Botany", P. Blakiston's Son and Co., Philadelphia*).

parts in multiples of four or five as opposed to the construction of the monocotyledonous flower, which is typically on the plan of three.

The dicotyledons, which include over 100,000 species, are generally divided into two main groups; the more primitive *Archichlamydeae*, in which the calyx and corolla are either very

poorly developed, or have their various members entirely separate from one another, and the *Sympetalae*, in which the petals are typically united into a *gamopetalous* corolla.

Of the great array of groups which compose the dicotyledons we shall mention only the most important. The Archichlamydeae include, among others, the following orders:

Amentiferae.—This group is now commonly divided into a number of subordinate orders, but in its larger sense it includes the oaks, beeches, chestnuts, hickories, walnuts, birches, alders,

FIG. 233.—One of the Ranales. Hepatica (*Hepatica triloba*), belonging to the family Ranunculaceae.

FIG. 234.—One of the Rosales. Choke cherry (*Prunus virginiana*), belonging to the family Rosaceae.

willows, poplars, and many others, all of them trees or shrubs. The perianth is scale-like or absent, the flowers dry and chaffy and arranged in a long, sometimes cone-like inflorescence, the *ament* or *catkin* (Fig. 107). They are prevailingly wind-pollinated. These plants were long regarded as the most ancient of the dicotyledons, but are now looked upon by many botanists as simplified and reduced forms.

Ranales (Fig. 233).—This great and varied group contains the buttercup, magnolia, laurel, and water-lily families and their allies, including trees, shrubs, and herbs. Its flowers are pollinated by insects and are primitive in the sense that their parts,

particularly the stamens and carpels, are typically numerous and have not become stereotyped in number and arrangement as is often the case among higher orders. The Ranales are regarded by many as the most ancient of the dicotyledons and as the center of origin for many of the higher groups.

Rosales (Fig. 234).—This huge order includes the saxifrage, rose, and legume families and their allies, comprising trees, shrubs, and herbs. The flowers are for the most part conspicuous and attractive, and furnish a large number of our ornamental plants. Many important fruits and vegetables also find their place here.

Fig. 235.—One of the Umbellales. Wild carrot (*Daucus carota*), belonging to the family Umbelliferae.

Fig. 236.—One of the Rubiales. Button-bush (*Cephalanthus occidentalis*), belonging to the family Rubiaceae.

Regularity and symmetry characterize the flowers of the lower members but in the legume family (Leguminosae) the corolla becomes markedly irregular, producing the butterfly-like or *papilionaceous* type.

Umbellales (Fig. 235).—This includes the dogwood family (mostly shrubs) and the carrot family (mostly herbs). The ovary in the group is inferior, the other floral parts being fused with it or borne upon it. The flowers are very small and arranged in compact, flat-topped clusters called *umbels*. This

order marks the highest point of development among the Archichlamydeae.

The following orders are most important among the Sympetalae:

Ericales (Fig. 109).—These are the heaths, mountain laurels, blueberries, and their allies, most of them shrubby plants, including many evergreens. The order is intermediate, in certain of its characters, between Archichlamydeae and Sympetalae.

Tubiflorales (Fig. 104).—Here are placed the morning-glory, phlox, borage, verbena, nightshade, mint, and figwort families and a number of others, most of the members of which are herbs. The corollas are conspicuous and prevailingly tubular, and are regular in the lower families but extremely irregular in the higher ones. The order comprises not only many of our garden flowers but a number of such important crop plants as the potato and tobacco.

Rubiales (Fig. 236).—Here are the madder and honeysuckle families, which are prevailingly trees and shrubs, although herbaceous species also occur among them. The flowers are most commonly on the plan of four and tend to be grouped in compact clusters.

Campanulales (Fig. 239).—This order includes the gourd, bellwort, and composite families, most of the members of which are herbaceous. The last is the largest and most widespread family among angiosperms. Its flowers are arranged in complex heads, each of which somewhat resembles a single flower, the flowers at the margin of the head often being different from those in the center. The calyx is greatly reduced and becomes a scalelike *pappus* surmounting a single-seeded ovary. This family is a remarkably successful one and marks the highest point in evolutionary advance among the dicotyledons.

Monocotyledoneae or Monocotyledons.—These plants, of which there are some 30,000 species, are characterized by the possession of a single cotyledon in the embryo, closed or parallel venation in the leaf, scattered vascular bundles in the stem, and a floral plan based on multiples of three. The group probably arose from somewhere among the primitive dicotyledons and its evolutionary advance has been more or less parallel with that of the latter group. With the exception of one order, monocotyledons are all herbs. Among the important orders are the following:

Glumales (Fig. 237).—These are the grasses and the sedges. The small flowers lack a typical calyx and corolla, are protected by chaffy bracts, and are arranged in clusters. They are wind-pollinated, except for those cases where pollination is affected directly, without external agency. As in the Amentiferae, their simple condition may have come about through reduction. The grass family includes the most important of our crop plants.

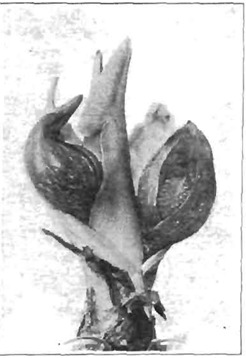


FIG. 237.—One of the Glumales. A sedge (*Carex*), belonging to the family Cyperaceae.

FIG. 238.—One of the Arales. The skunk cabbage (*Symplocarpus foetidus*), belonging to the family Araceae.

Palmales.—The palms are a tropical tree-like family in which the columnar trunk is surmounted by a cluster of large leaves. The small flowers are borne in spikes and in some species are pollinated by wind and in others by insects. The perianth is very simple.

Arales (Fig. 238).—These are the aroids, a family of large herbs particularly abundant in the tropics and represented with us only by the Jack-in-the-pulpit, skunk's cabbage, and a few other species. The leaves are typically large, and, unlike those of most monocotyledons, are netted-veined. The very simple flowers, almost devoid of a perianth, are clustered on a fleshy *spadix* which is enveloped by a large and often brilliantly colored bract, the *spathe*.

Liliales (Fig. 98).—These include the lily, amaryllis, and iris families, perennial herbs with well developed bulbs or rootstocks. The species usually have a conspicuous perianth and provide some of our most beautiful garden flowers.

Orchidales (Fig. 240).—The orchids are notable for the extreme irregularity and great beauty of their flowers, and their remarkable specializations for insect pollination. They are particularly abundant and brilliant in the tropics, whence they have been introduced into the greenhouses of cooler climates as the most highly prized of exotics.

Fig. 239.—One of the Campanulales. Yellow chamomile (*Anthemis tinctoria*), belonging to the family Compositae.

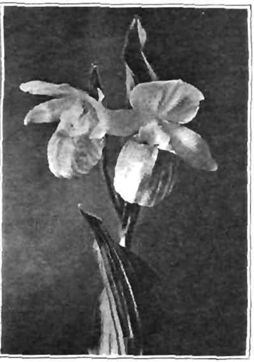


Fig. 240.—One of the Orchidales. Showy lady's slipper (*Cypripedium hirsutum*), belonging to the family Orchidaceae.

With the development of the composite and orchid families, the plant kingdom has reached the climax of its evolution.

QUESTIONS FOR THOUGHT AND DISCUSSION

790. Why have plants which reproduce by seeds rather than those which reproduce by spores become the most successful part of the world's vegetation?

791. Can you suggest why seed plants have so very many more species than either bryophytes or pteridophytes?

792. From a consideration of the present distribution over the earth of ferns and of primitive seed plants, what suggestion can you make as to the climatic conditions under which the earliest seed plants were evolved?

793. Why do you think it is that seed plants are not very common in the ocean?

794. The name "Flowering Plants" is sometimes applied to the seed plants. Why is it not a very satisfactory name?

795. The archegonium is much reduced in the gametophyte of the seed plants. Explain.

796. With what in the ferns is the embryo-sac of seed plants comparable? the pollen grain? the ovule? the nucellus?

797. To what in seed plants do the following structures in liverworts correspond: The spores; the sporangium wall and seta; the thallus; the sperms?

798. Different terms are used for the various structures in the plant's life history among seed plants than are used among bryophytes and pteridophytes (embryo-sac for female gametophyte, anther for sporangium, and so on). What reason can you suggest for this?

799. What great groups of animals are there which obtain the bulk of their food directly or indirectly from other plant groups than the seed plants?

800. What similarities can you suggest in the evolutionary history of bryophytes, pteridophytes, and spermatophytes, in the plant kingdom, to that of amphibians, reptiles, and mammals in the animal kingdom?

801. What various resemblances do the cycads show to the ferns?

802. In what way is the relation of the conifers to the rest of the gymnosperms similar to that of the ferns to the rest of the pteridophytes?

803. What relation can you suggest between the characteristic wood structure of the conifers and the tough and scale-like character of their leaves?

804. In such a tree as the pine, are the staminate or the ovulate cones more numerous? Explain.

805. In regions where there are large coniferous forests, "showers of sulphur" sometimes occur in the spring. What explanation can you suggest for these?

806. What advantages have the angiosperms over the gymnosperms which should have made them so much more successful?

807. Give an example of a crop plant which is an annual herb; one which is a biennial herb; one which is a perennial herb; one which is a shrub; one which is a tree.

808. Which of these five plant types is of most importance in agriculture? Why?

809. There is a larger proportion of herbaceous species in the flora of a temperate region than in the flora of a tropical one. Explain.

810. Angiosperms, and especially herbaceous angiosperms, have apparently evolved much faster and given rise to many more species than either pteridophytes or gymnosperms in a similar length of time. Why?

811. What evidence can you suggest for the conclusion that the dicotyledons are more ancient than the monocotyledons?

812. We believe that families in which the flowers are irregular are usually more recent in evolutionary origin than those where the flowers are regular. Why?

813. We believe that a flower with a large and indefinite number of floral parts, all free from one another, is more ancient in type than one in which the number of parts is smaller and more constant and where they are more or less united with one another. Why?

814. In what respect may stamens and carpels be called "sexual organs" and in what respect is it incorrect to call them such?

815. What conclusion can you draw as to the relative osmotic concentration of the cell sap in the pollen grains and in the cells of the stigma?

816. Why do we regard the composite and the orchid families as marking the highest points in the evolution of the plant kingdom?

REFERENCE PROBLEMS

138. What family is most important as a producer of food plants and what are some of the notable crop plants included in it? Name a few other families which have many important economic plants.

139. Seed plants are sometimes known as the *Siphonogamia*. Why is this name appropriate for them?

140. The terms *Cryptogams* and *Phanerogams* are sometimes used to designate two groups into which the plant kingdom may be divided, the

former including thallophytes, bryophytes, and pteridophytes, and the latter including seed plants. Why is such a classification not a very good one?

141. Name five cultivated plants which belong to the rose family; five which belong to the nightshade family; five which belong to the composite family.

142. What family of plants is most important as far as the production of cultivated fruits is concerned?

143. What family of plants is most important as far as the production of timber is concerned?

144. Give the derivation of the following terms and explain in what way each is appropriate:

Antipodal Cells　　Synergid　　Papilionaceous

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